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Life History and Morphology of the Immature Stages of the Bog Copper butterfly *Lycaena epixanthe* (Bsd. & Le C.) (Lepidoptera: Lycaenidae)

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Abstract. The first complete life history of *Lycaena epixanthe* (Bsd. & Le C.) is presented along with an ultrastructural examination of immature stages using scanning electron microscopy. The butterfly is strictly endemic to cranberry bog habitats and closely alligned with the biology of its foodplant *Vaccinium macrocarpon* Ait. Reproductive biology of adult butterflies is linked to the hostplant flowering period and the microanatomy of ova, larvae, and pupae show fine adjustments for survival in the bog. Despite its unique features, *epixanthe* is an integral part of the lycaenine group. Basic characteristics of immature and adult butterflies show close behavioral and developmental similarities with other *Lycaena*.

Introduction

The cranberry-feeding *Lycaena epixanthe* (Bsd. & Le C., [1835]) is a diminuitive Nearctic lycaenid generally considered endemic to bog habitats. The current known range of *L. epixanthe* corresponds closely with the extent of recent Pleistocene glaciation in the eastern half of North America and includes a few refugia south of the glacial terminus on the coastal plain and in the Appalachian mountains (Wright, 1982b). Continental glacial action at its peak displaced northern biota far to the south and during is retreat left behind many poorly-drained depressions and kettles which became the boggy peatlands that harbor today's unique bog flora. Many acid-loving ericaceous plants flourish in these bogs, including large cranberry *Vaccinium macrocarpon* Ait. and small cranberry *V. oxycoccos* L. The butterfly is tied strictly to bog habitats where cranberry can grow and its biology is totally adapted to its relationship with this plant. On the whole, the life history of *L. epixanthe* is still quite fragmentary and nearly all present-day lepidopterological literature describes the immature stages as largely unknown. The intent of this study is to present details of *epixanthe*'s life history and to describe the microanatomy and chaetotaxy of the immatures using scanning electron microscopy.

Historical Synopsis of Previous Works

Brief aspects of historical studies on the life history of *L. epixanthe* have

been summarized previously by Wright (1982a). The search for the foodplant and immature stages brought repeated failures to many who had sought them. In some of his very first writings, Scudder (1868, 1869, 1872) noted that *epixanthe* adults were associated with cranberry and even nectared on the blossoms. Yet he persisted to believe throughout his career that the foodplant was one of the Polygonaceae, particularly swamp dock *Rumex verticillatus* L. (Scudder 1876, 1889, 1893). Guesswork by many early authors lead to several erroneous foodplant entries in Tietz's (1972) life history compendium. The foodplant was eventually discovered in 1907 by Cook and Watson (1908) who observed oviposition firsthand on *Vaccinium macrocarpon* in New Jersey. Since the discovery of the foodplant, the immature stages have received very little attention and no single work is complete. The white echinoid ova were first described by Saunders (1869) and later by Scudder (1889), both from artificially obtained ova. Scudder (*loc. cit.*) included three illustrations of ova in his voluminous work (Pl. 65, Fig. 16 & 23; Pl. 68, Fig. 11), but his first figure was unrecognizable and contrastingly different than the latter two. This discrepancy can be attributed to the fact that Scudder commissioned several artists to render illustrations. Scudder (*loc. cit.*) also examined a "dead and dried" first instar dissected *ex ovum* from which he gathered very little detail. His attempt to picture the head capsule (Pl. 79, Fig. 41) yielded a paucity of cranial setae and an inaccurate fronto-clypeal apotome. It was not until many years later that live larvae were actually observed for the first time. Franklin (1948) in the miscellaneous section of his "Cranberry Insects in Massachusetts" published a photograph of an *epixanthe* mature larva and pupa. The photograph was not accompanied by descriptive text and stood alone with legends only. Despite its shortcomings, Franklin's photograph was the first of its kind and it went virtually unnoticed by the lepidopterist community. Plath (1978) was the first to successfully undertake a rearing study of *epixanthe*. Unfortunately, his sketchy paper described only a brief three-instar larval development in which the "date of hatching was not known." It is now confidently known that *epixanthe* has a four-instar larval development and Plath's instars were mislabeled after the crucial first instar was missed.

Materials and Methods

The study site was Forge Pond bog in the New Jersey pine barrens where an *epixanthe* colony was discovered in 1976 and has been under continuous investigation since. Forge Pond lies adjacent to Nescochague Creek in the southwest corner of the Wharton State Forest (Atlantic Co.) and can be located on the USGS Atsion Quadrangle (7.5 min. series) at 39 38'55" N latitude, 74 40'05" W longitude. The bog is an abandoned meander of the nearby stream and is best characterized as an oxbow bog. Water depth is generally very shallow and maintained by seepage from the high water table of the underlying sandy soils. To a certain extent, stream overflow following heavy rains also contributes to the water level. The flora is very

typical of New Jersey pine barren bogs where marsh-like vegetation is dominated by open wet stands of sedges and sphagnum ground cover. Chief sedges at Forge Pond are coastal sedge *Carex exilis* Dewey, twig rush *Cladium mariscoides* (Muhl.), and white beaked-rush *Rhynchospora alba* (L.). The sphagnum bog flora is very acidic and supports a luxurious growth of cranberry *Vaccinium macrocarpon* Ait. which grows as a low trailing vine running over the surface of the bog between sedge blades. Dwarfed cedar trees *Chamaecyparis thyoides* (L.) appear occasionally in the center of the bog, but generally they form thick stands of taller trees around the bog perimeter. A diverse association of herbaceous bog flora, including carnivorous plants and orchids, blooms in the wetter areas of the bog throughout the warmer months. Further details of the Forge Pond flora may be found in Thomas (1967).

In 1981, the *epixanthe* colony was observed throughout its entire flight period (12 June to 10 July) with careful attention paid to the biology of adult butterflies (e.g. basking, nectaring, courtship, pairing, oviposition). Where possible, interesting facets of adult life were recorded on 35 mm film for re-examination at later dates. A few freshly oviposited ova (three) were marked in the bog for identification in the following spring of 1982. A second larger batch of ova (198) was obtained for rearing studies by artificially confining seven gravid females (captured 22-24 June) with their foodplant in a wooden rainbarrel. The rainbarrel measured one meter in height and one meter in width, and contained an intact segment of the bog surface removed *en bloc* from the natural bog. Wire screening covered the opening at the top of the barrel. After confined females had expired, the total number of ova was counted and an average index of fecundity (ova/female) calculated. Diapausing ova remained outdoors throughout the study to assure that ambient temperatures and weather conditions were as close as possible to the natural state. Water was added periodically to the barrel to maintain moisture in the sphagnum covering and cranberry leaves. In a separate experiment, six cranberry shoots with their ova were clipped and removed from the rainbarrel and maintained in open glass jars without water. This was done in order to determine the effect of lack of moisture on ova viability.

Once hatching began in the spring of 1982, larval development was followed carefully in the natural bog and under experimental conditions. To ensure proper collection of individual larval data in the rearing experiment, tiny first instars were removed from the rainbarrel and transferred to individual potted plants. These plants were propagated from natural cranberry and rooted in soil consisting of half sand and half peat. They required regular watering and fertilizing (Osmocote). Developing larvae and pupae were examined several times daily and photographed to permanently record their growth, coloration, and behavior. Approximately six representative specimens of each larval instar and the same number of pupae and ova were submitted for scanning electron microscopy (SEM). A few exuviae of fourth instars were similarly examined.

SEM of ova, larvae, and pupae was performed with a Philips SEM 500 (Eindhoven, Holland) using an accelerating voltage of 25 kV and tilt angle of zero degrees. For studies of ova, individual cranberry leaves with an ovum attached were mounted directly onto SEM stubs using double-sided tape and then coated with 360 A° of gold-palladium (40/60) in a Polaron E-5000 sputter coater (Hertfordshire, England). Larval exuviae were mounted and coated in the same fashion. All live larvae and pupae were first fixed and then critical-point dried prior to coating. This

was done to prevent shrinkage of soft tissues and to help ensure accurate morphological determinations. Larvae and pupae were fixed in 3% buffered glutaraldehyde (pH 7.2 with 0.1M sodium cacodylate buffer) for two hours at room temperature (22-25°C). Occasionally, some of the larger specimens (fourth instars) were fixed overnight in the refrigerator (4°C). Refrigerated samples were allowed to warm to room temperature prior to dehydration. All fixed samples were dehydrated in a graded series of acetone (30-100%) with approximately five minutes in each acetone strength before transfer. Following dehydration, they were promptly placed in a liquid CO2 chamber and critical-pointed dried after the acetone had been flushed from the tissue. They were then promptly mounted onto SEM stubs with double-sided tape or conductive paint for larger specimens and sputter-coated with 360A° gold-palladium (40/60). Earlier instars were mounted still attached to cranberry leaves which acted as a convenient vehicle for transfer. Most specimens were examined immediately in the SEM. Some were held in dessicant jars containing granular phosphorus pentoxide (Granusic). Under such conditions, they could be stored for long periods of time without deterioration. All SEM photographs were taken with Polaroid 55 positive-negative film.

Ultraviolet photography (UV) was used to study pinned adult specimens following the method of Ferris (1972, 1975). A 35 mm single lens reflex camera with Wratten 18A filter (Kodak) recorded images of UV reflectance on 400 ASA film (Tri-X). The specimens were illuminated by two 15-watt blacklight blue bulbs (Westinghouse) at a distance of six inches.

All setal maps of larval cranium, body, and prothoracic shield were reconstructed from SEM micrographs. In describing the chaetotaxy, the terminology and conventions of Hinton (1946) were heavily relied upon. Hinton's work is the nomenclatorial system familiar to most larval workers. With a few minor modifications for the cranium (Hinton, 1947) and prothoracic shield (Hinton, 1956), Hinton's system is still very suitable for current larval studies. Downey has adapted the Hinton system for use with lycaenid larvae (Lawrence and Downey, 1966; Downey and Allyn, 1979) and the present study used the Hinton system in much the same fashion. Parenthetically, it should be stated that usage of this system was for the convenience of naming setae only. Setal origins and homologies were not implied. Terminology of ova morphology conformed to that used by Downey and Allyn (1981) in their survey of lycaenid ova. Terminology of pupal stridulatory and associated structures followed that of Downey (1966) and Downey and Allyn (1973). All generic names of butterflies were from Howe (1975) where Nearctic lycaenines were placed in the single genus *Lycaena*. Generic names of Scudder (1876) and Miller and Brown (1979, 1981) were regarded as subgenera. Plant names followed 8th edition Gray's Manual of Botany (Fernald, 1950). For proper spellings and dates of Boisduval and Le Conte's *Hist. Lepid. Amerique sept.*, the in-depth study of Cowan (1969) was consulted.

RESULTS

Biology of Adults

In six continuous years of study (1976-1981), emergence of adult butterflies was uniquely timed to occur with the beginning of the cranberry flowering period. Furthermore, the full duration of the hostplant flowering period and butterfly flight

period closely paralleled one another from year to year. The flight period averaged about four weeks. Males appeared first and were followed several days thereafter by females. Peak numbers of males and females appeared in the second and third weeks. Towards the end of the flight period, females predominated, and usually during the last week of the flight period only worn females could be seen. In 1981, the first males appeared on 12 June and the last female was seen on 10 July.

Individual butterflies were invariably associated with cranberry plants all day long and seldom were seen far from the hostplant. They nectared almost exclusively on cranberry blossoms throughout the day (0900-1900 hrs.) and only on two occasions was another nectar plant observed being used. Both observations occurred early in the flight period when two males briefly visited goldcrest *Lophiola americana* (Pursh) growing in the center of the bog. In addition to nectaring, many adults were also seen imbibing drops of water trapped on sedge stems and the sphagnum surface. This behavior seemed deliberate especially on very hot days, when they probed the vegetation surface with their proboscis presumably in search of moisture. During cranberry flowering, the diversity of bog butterfly fauna was limited and interspecific competition for nectar resources was minimal. In addition to *epixanthe*, the sedge-feeding hesperiids *Euphyes dion* (W. H. Edwards) and *E. bimacula* (Grote and Robinson) were present in small numbers; and the marsh grass satyrid *Euptychia areolatus septentrionalis* (Davis), while occasionally abundant, did not nectar. Honeybees and bumblebees were the primary cranberry pollinators. On occasion, their busy activity displaced nectaring *epixanthe* adults from cranberry blossoms. Generally blossoms were so numerous that butterflies were never excluded from nectar.

Courtship and pairing always took place in the vicinity of cranberry. In search of potential mates, males perched and darted out to investigate passing objects. While cranberry was the preferred perching plant, a few males were seen perching on sedges, goldcrest, and small cedar saplings. Both males and females began early morning basking around 0800. Following this, males generally began to perch about 1000 with many of them continuing to bask simultaneously as they perched. Peak perching activity took place in the early afternoon and gradually stopped around 1800. Perching was intermittently interrupted to nectar on cranberry blossoms. After 1800, both males and females showed little interest in courtship and spent their time nectaring and basking in the setting rays of the sun. The sun tended to "set" early in the bog due to the border of tall surrounding cedar trees.

When perching males flew out to investigate a passing butterfly, a brief spiral encounter usually occurred. If the subject investigated was another male, the encounter ended quickly. If it was a female, she usually landed promptly within seconds after the beginning of the encounter flight. Following this, the courting male landed quickly behind her, initiated a flurry of rapid wing vibrations, and attempted copulation within seconds. An unreceptive female flapped her wings strongly as part of a "rejection signal" which indicated she was previously mated. Most males promptly flew away after seeing the female's flapping wings. However, if the female was receptive, she was quiescent and copulation would take place immediately (Fig. 1). Most copulations took place on cranberry vines or redroot *Lachnanthes tinctoria* (Walt.) (Fig. 1) and were observed in the early afternoon hours (1200-1400) during peak male perching activity. A rare late afternoon mating (1615) was noted on one occasion. One coupled pair was observed in flight with the larger female leading.

Coupled butterflies usually remained *in coitu* for approximately thirty minutes. Oviposition commenced two to three days after mating.

Oviposition was observed to occur mostly in the late morning to mid-afternoon (1100-1415). The technique of oviposition was characteristic. Females typically selected cranberry plants at the edge of the bog where the hostplant was densely covered and hidden by sedges, particularly *Carex exilis* Dewey and *Cladium mariscoides* (Muhl.). After first landing on the sedges, the females then walked down the sedge stems nearly disappearing from sight. When they reached the hidden cranberry vines below, they transferred to the hostplant and selected a single leaf about three to eight cm. from the tip of a fresh shoot where they deposited a single ovum on the leaf undersurface. Most of these ova came to rest about ten to twenty cm. above the sphagnum surface of the bog floor. On occasion, ovipositing females were observed to nectar on the same cranberry plant upon which they had just oviposited or were about to oviposit. Under experimental conditions, seven gravid females confined within the cranberry-containing rainbarrel oviposited 198 ova yielding an index of fecundity of approximately 28 ova/female.

Adult *epixanthe* from Forge Pond bog were polymorphic for ventral coloration, a condition observed in each year of study. Although yellow is the typical ventral color for the eastern subspecies *L. e. epixanthe*, the Forge Pond population had small numbers of both sexes which were gray to gray-white (Fig. 1). This gray morph accounted for approximately 5% of the population and did not exhibit any noticeable behavioral differences. The yellow/gray polymorphism was not confined to Forge Pond and was uniformly noted in series of *epixanthe* collected in several other bogs within the New Jersey coastal pinelands. The low-frequency gray morph was compared with the holotype and a long series of the typically gray midwestern subspecies *L. e. michiganensis* Rawson. The two were virtually indistinguishable.

Adult butterflies at Forge Pond demonstrated the expected sexual dimorphism in ultraviolet (UV) reflectance. Males showed very strong UV reflectance in the discal regions of both dorsal wing surfaces (Fig. 9). This reflectance corresponded very closely with the "visible" wing iridescence seen with the human eye in the proper angle of sunlight. The male's discal UV reflective areas were surrounded by a broad border of non-reflective black, especially on the DHW. The female was entirely non-reflective in the discal regions. Some females had a short row of inner submarginal HW lunules which reflected stongly in UV (Fig. 10). In visible light, these scales were light silver in color and scarcely perceptible. They were immediately medial to the orange marginal lunules and the series of submarginal black maculations. Maculations and veins of neither sex were reflective in UV.

Biology of Immatures

Newly oviposited ova were bright pure white in color (Fig. 2), but dulled very slightly after a few days as the embryonic larva developed. This was most noticeable in the depth of the chorionic pits and micropylar region where chorionic thickness was minimal. Two ova were dissected at 10 days of age showing embryonation complete and fully-developed first instars present. These larvae were quiescent and appeared to be in diapause. None of the remaining ova hatched until the following spring. Six cranberry shoots that were clipped and removed from the rainbarrel were completely dessicated within one week's time; diapausing larvae within the ova were also dessicated and dead.

In the following spring (1982), winter-like conditions lingered into April. Snows occurred on 6 and 9 April, and cool weather kept daytime maximum temperatures at 4.4°C (40°F). A slow warming trend began on 11 April and peaked on 16 April with a high temperature of 23.3° C (74° F). First instar larvae began emerging on 16 April and continued emerging until 27 April. Emergence took place through a small exit hole chewed in the top of the ova. No further feeding on the eggshell was noted. Tiny first instars were very mobile from the start and generally moved to positions on other cranberry leaves within minutes. Resting concealed on ventral leaf surfaces (Fig.3), first instars ate holes in the undersurface parenchyma. A protrudable head and neck made it possible for the larvae to widen and deepen these holes, but the upper epidermal surface of the leaf was never broken. Leaves bearing these holes quickly became discolored and displayed small brown blotches when viewed from above. Scanning the cranberry leaves for these blotches became a very good search method to locate larvae. Usually three to four holes were made per leaf. (See leaf at bottom of Fig. 3). Larval movement was not confined to leaves of a single vine. All instars moved freely onto adjacent vines at points of contact. (Mature instars were even seen crossing 1-2 cm. of sphagnum in order to reach another vine.) Feeding, as a rule, took place during warm daylight hours and larvae rested at night. Freshly molted larvae did not consume exuviae.

Second instars, like the first, fed almost exclusively while concealed on the ventral leaf surfaces (Fig. 4). Both first and second instars have bold dorsal red stripes patterned against a green body color. This provided a large element of camouflage for the young larvae as they blended with the green leaves and red stems of the cranberry plants. A few slow- developing second instars were still present at the time when new cranberry shoots began to unfurl (mid-May). These instars were able to eat entire leaves at the tip of the supple shoot and, even though exposed in this situation, they were still nicely camouflaged.

Third and fourth instars fed entirely on new tender shoots (Figs. 5 & 6). They were now large enough to eat full-thickness leaves and fourth instars even consumed stems and an occasional embryonic flower. Third instars had a small residual dorsal red stripe, while fourth instars were solid green. Even though these larvae remained openly-exposed in their positions on the new shoots, they were extremely difficult to detect. Their green body surface had a distinct matt appearance which produced considerably less spectral reflectance than earlier instars. No larval predators or parasitoids were observed and at no time were larvae attended by ants.

Nearing time for pupation, fourth instars selected the underside of a low-lying cranberry leaf on which they spun a silk pad for cremastral hooks and an arched silk girdle for pupal support. The girdle usually came to lie in the dorsal intersegmental groove between the second and third abdominal segments. Although fourth instars at maturity (15 mm.) were somewhat longer than most cranberry leaves, the prepupal larvae (Fig. 7) contracted considerably to conform to average leaf size (9 mm.). The green-colored pupae (Fig. 8) were speckled with black spots and remarkably well-concealed beneath the cranberry leaves close to the sphagnum surface. Some pupae were actually temporarily hidden within the sphagnum when the moss expanded after heavy rains. An interesting polymorphism for pupal color was noted. Approximately 5% of the pupae were solidly dark purple in color without noticeable black speckling. Purple pupae yielded normal yellow adults. No ants were seen with the pupae and stridulatory pupal sounds were not heard in the bog.

Stridulation in experimental conditions is still under investigation.

The total period of development from larval emergence to adult eclosion ranged from 52-60 days (ave. = 54). The four-instar larval period averaged 41 days and the pupal period 13 days. Average duration of each larval instar was 11, 9, 7, and 14 days respectively. Each instar terminated with a one to two-day period of inactivity prior to molting. The rate of growth during each instar, exclusive of pre-molt quiescence, was respectively 0.12, 0.36, 0.60, and 0.58 mm./day. In accordance with Dyar's rule (Dyar, 1890), there was a regular progression of head-capsule widths during larval development: first, .250-.285 mm; second, .380-.400 mm; third, .625-.640 mm; and fourth, 1.025-1.077 mm. Eclosion took place during daylight hours (0730-1600) and began on 7 June and lasted to 26 June.

Of the original 198 ova in the rearing experiment, 19 were destroyed by pill bugs (Isopoda) in the rainbarrel, 10 were traumatically displaced and lost during handling, six were submitted for SEM, six were used in the hostplant dessication experiment, and two were dissected to examine diapausing larvae. The remaining 155 ova overwintered, but only 56 produced live larvae. Fourteen ova contained dessicated dead larvae and the remaining 85 ova were sterile, most likely from unmated females. Of the 56 live larvae, 36 larvae and pupae were sacrificed for SEM and the remaining 20 eventually produced normal adults (12 males and 8 females).

Morphology of Immature Stages

OVA

The eggs of *L. epixanthe* (Figs. 2 & 14) were upright, dome-shaped, and typical of the lycaenine type; they were round in upper view and echinoid in lateral view with the upper surface gently convex and the bottom surface flattened. The light-colored sculpturing (reticulum) of the outer chorion supplied the ova with a honeycombed or pitted appearance. The depressed pits, properly called cells, were formed within a network of intersecting chorionic ridges (muri). The ridges formed the wall-like sides of each individual cell and created small rounded prominences at points of intersection. In addition to the general configuration of the chorionic reticulum, it was not uncommon to find tiny strands of chorionic secretion (streamers) scattered irregularly over the egg surface. Measurement of six ova provided an average width of 0.75 mm and height of 0.48 mm.

The micropylar area (Fig. 18) was depressed and located in the central axis on top of the egg. It measured 0.08 mm in diameter and 0.06 mm in depth. On low power magnification, it appeared as a typical cell on the upper surface of the egg and did not influence the egg profile. The micropyle proper (Fig. 19) was a very small centrally-located, five-sided depression (pentagon) found at the bottom of the micropylar cell. Five tiny holes were located at the apices of the pentagon just beneath the lip margin. These holes varied from 0.4-0.8 microns in diameter. The pentagonal depression measured 5 microns in greatest diameter.

Figs. 1-8. Life history of *Lycaena epixanthe* (Bsd. & Le C.). Forge Pond bog, Atlantic Co., N. J. **1.** Yellow female and gray male mating, 21-VI-1981, 1.5 x. **2.** Ovum on undersurface of cranberry leaf. 13 x. **3.** First instar, 5 x. **4.** Second instar. 4 x. **5.** Third instar, 4 x. **6.** Fourth instar, 3 x. **7.** Pre-pupa, 5 x. **8.** Pupa, 5 x.


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2


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6


7


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Encircling the central micropyle depression was a rosette of petal-shaped cells which varied individually in size and shape (Fig. 18). Variability in rosette morphology from egg to egg was not uncommon in that some eggs had four cells to the rosette and others had five. Chorionic thickenings and bumps were frequently noted on the floor of rosette cells and incidental chorionic streamers crossing this area were also common. Occasional groups of exfoliated follicular epithelial cells were also seen. Surrounding the rosette were secondary and tertiary rows of much smaller angulate cells, completing the micropylar annulus. At the outer margin of the annulus, the walls of the micropylar region rose abruptly separating the micropylar pit from adjacent cells. There appeared to be ample air space communication between the micropylar pit and the system of air spaces beneath the sculptured chorion. Communication was accomplished via aeropyles in the annulus, open lateral recesses of annulus cells, and larger openings in the vertical side walls of the micropylar pit itself.

The system of ridges and cells covering the remainder of the egg surface followed a faint geometric pattern found in many other lycaenid ova (Figs. 14 & 15). Ridges were positioned in a series of involute curves which began at the micropylar region and coursed diagonally over the upper surface of the egg and similarly down the sides of the egg. When viewed from above, they radiated from a central axis in the fashion of a spiral nebula. Tandem pairs of curving ridges formed the opposite walls of each individual cell and, where they intersected with other ridges, formed rounded prominences. Generally, four prominences surrounded each cell and the ridge connecting each prominence had a single deep undulation. On occasion, a thin membrane of chorionic material supplied the connection in this area (Fig. 16).

The individual chorionic cells were cup-shaped and nearly circular when viewed from above (Fig. 16). They averaged 0.06 mm wide at the cell mouth and 0.02 mm wide at the base; average depth was 0.06 mm. On low magnification SEM (Fig. 15), the surfaces of the surrounding ridge tops were smooth in appearance. No aeropyles were noted on the ridges or at ridge intersections. However, at higher magnification (Fig. 6), the ridge chorion was seen to be porous containing a diffuse scattering of tiny, almost imperceptible perforations. These perforations (less than one micron in size) communicated with a network of small air spaces immediately beneath the chorionic surface (Fig. 17). Numerous perforations of larger size were located deep within the basal half of each individual chorionic cell (Fig. 16). These holes (aeropyles, plastronic pores) occurred in clusters of 20-30 per cell and averaged about 2.5 microns in diameter. They communicated with still larger airspaces beneath the chorionic surface.

The chorion in cross-section was a two-layered structure that appeared to function as an air-trapping device (Fig. 17). The inner chorion (4 microns thick) was smooth and formed a protective sphere around the oocyte and vitelline membrane. It was uniformly solid except for a small area of entrapped spongiform air cells on the dorsum of the egg surrounding the micropylar region. The inner chorion also provided support for the characteristic reticulations of the outer chorion. Intrachorionic airspaces were clearly grouped into two major subdivisions. The first and largest subdivision consisted of a series of tall chambers next to the inner chorion, partitioned by thin vertical walls of chorionic material. This subdivision occupied the lower two-thirds of the intrachorionic cross-sectional area and had direct communication with the exterior via aeropyles in the chorionic cells. The second

and smaller subdivision was situated immediately beneath the highest portions of the arching ridges and contained an intricate meshwork of chorionic spokes. This subdivision communicated with the exterior via fine porosity in the surface chorion of the ridges. The two airspace subdivisions also communicated with one another by small scattered aeropyles. The entire airspace trapped between the outer and inner chorion was continous and covered the entire surface of the egg except for the flattened bottom which was appressed to the hostplant. The flat bottom contained only a smooth inner chorion.

LARVA: FIRST INSTAR

General. The fully-developed first instar within the ovum measured 1.4 mm in length prior to hatching and 2.5 mm at the end of the stadium immediately prior to the first molt. Larval shape was nearly cylindrical at emergence, but assumed classical onisciform shape within the first day (Figs. 3 & 20). Body color was uniform light yellowish-green at emergence, but thereafter quickly deepened (green) and developed distinctive stripes within a few days. Stripe pattern consisted of a series of alternating red and white longitudinal lines on the major body regions (dorsal, subdorsal, lateral). (See Fig. 3). On the mid-dorsum was a bold red stripe that started on the mesothorax and continued over the abdominal segments. Prominent arching dorsal setae originated in this dorsal red stripe. (See chaetotaxy below.) At the seventh abdominal segment of several larvae, the stripe broadened and diffused over remaining segments creating a red smeared appearance. In the subdorsal region there was a series of four smaller longitudinal lines. First, a thin white line rested against the dorsal red stripe, followed in descending order by a faint broken red line, another thin white line, and a final broken red line. All of these small subdorsal lines started on the mesothorax and terminated near the seventh or eighth abdominal segment. Subdorsal and supraspiracular lenticles were incorporated into the two broken red lines. Below the subdorsal region, the lateral body area was mostly unmarked. A few larvae had an extra faint white line coursing through the abdominal spiracles, plus a row of faint subspiracular red dots (one per segment). In all larvae, the lateral ridge bore a skirt of laterally-projecting prominent setae and a bold white stripe from the mesothorax to the last abdominal segment. All chalazae were brown in color, as were the spiracles. The outer perimeter of the lenticles was brown, but the central portion was membranous and nearly concolorous with the integument.

Integument. The outer surface of the integument (epicuticle) had a surprisingly detailed microtopography revealed by the scanning electron microscope. In the fully expanded first instar, a large proportion of the surface integument was flat and oriented in one plane (Fig. 25). Spectral reflectance was great. Small tubercles, 2.5 microns wide and 2.0 microns high, were scattered evenly over the flat surface approximately seven to eight microns apart. Many of these tubercles terminated with a central microspine. In non-expanded first instars dissected *ex ova*, the epicuticle was contracted and wrinkled (Figs. 21 & 23). However, future tubercles could be seen at regular intervals within the wrinkled folds.

On low power magnification, a distinctive pattern of conical pits or dimples appeared in the integument on the lateral sides of each segment (Fig. 20). These pits were arranged in a regular fashion and their geometrical pattern was bilaterally symmetrical and showed no individual variation. Some pits were even present in

intersegmental grooves and appeared in the same position in all subsequent instars.

Integument sculpturing may eventually prove to be useful for comparative taxonomic studies and an effort was made to describe the integument of each instar. Besides the generalized pattern of sculpturing in each instar, specialized regions of the integument (spiracles, anal folds) contained their own unique sculpturing and are described separately.

Spiracles. Spiracles were delimited by a sclerotized ring which surrounded a circular opening. The interior wall of each spiracle contained sculptured chitinous projections that pointed centrally into the lumen. These structures were felt to be derivatives of the integument because of their superficial location and absence from deeper endotrachea. Their pattern was simplified and consisted of 20-25 straight blunt-tipped spines (1.5-2.0 microns in length) that circled the interior spiracular wall. Pointing inwardly, they formed an effective meshwork that protected the deep-seated tracheal system.

Cranium. The cranium was well sclerotized and deeply black pigmented. Typical of other lycaenids, it was hypognathous-projected and capable of being deeply retracted into the prothorax (Fig. 22). Average dimensions for the first instar were width .267 mm, length .225 mm, and height .160 mm. Anteriorly, the two arms of the adfrontal sutures did not meet before reaching the cervical triangle (Fig. 11A). The frons was thus "open" and extended dorsocaudad into the cervical musculature. In live preparations, the transparent cervical musculature was observed to insert anterodorsally onto the small apical portion of the frons and dorsolaterally onto a ridge on the posterior margin of the epicranium. The clypeus was distinct and located ventral to the frons. Ocelli were present as a group of six in a circle on the lateral aspect of the head capsule. Cranial appendages will be described separately below and the reader is referred to Figures 11 and 22 for this discussion. The ventral views of Lawrence and Downey (1966, Fig. 2C) and Downey and Allyn (1979, Fig. 1) are also helpful in interpreting these complicated structures.

Antennae: Antennae were three-segmented and originated from a membranous area (antacoria) between the head capsule and the mandibles. They did not differ radically from other lycaenid larvae and the pattern of sensory papillae was essentially idenical. The three segments together measured 25 microns in length and the long setae of the second segment measured 80 microns.

Labrum: The labrum consisted of a setae-bearing rectangular plate in the midline just ventral to the fronto-clypeal region (Fig. 11 C). The inferior margin was deeply notched. Average width was 95 microns. Six setae and a puncture were present on the anterior surface. (See chaetotaxy below.)

Mandible: The first instar mandible (65 microns length) had five teeth (Fig. 11 D). The first four teeth (numbered anterior to posterior) were incisor-like and angled medially. The fifth and most posterior tooth was rounded terminally. This tooth was juxtaposed to the posterior mandibular condyle and two laterally-projecting setae (10 and 25 microns) which originated from the posterior lateral mandibular margin. The oral surface contained a weak ridge (retinaculum) beginning at the condyle and terminating on the opposite mandibular margin. Minor sclerotized crests ran from the retinaculum to the teeth.

Maxilla: The maxilla with its associated bilateral palps was very similar to that of previously described lycaenids. The free sclerotized portion of the maxillary palps

contained three segments. The first segment supported a medial galea, a short forward-projecting seta (15 microns), and the remaining two palp segments. The galea and terminal palp segment contained the usual arrangement of sensory structures. The entire palp actually rested on a fourth sclerotized ring (palpifer) at its base, which in turn was attached to the membranous portion of the distal stipes (dististipes) on the ventral surface of the head. Additional setae were found on the palpifer (one, 20 microns) and sclerotized portion of the basistipes (two, 40 microns).

Labium: The membranous submentum resided between the two large lobes of the stipes (basistipes) and bore two ventral-projecting setae (30 microns). The sclerotized mentum was anterior to the submentum and its U-shaped arms surrounded the midline spinneret, palpiger, and paired labial palps. It then extended dorsally to parallel the hypopharynx. On the proximal portion of the mentum there were two small setae (5 microns), one on each side of the spinneret. The labial palps consisted of two segments, each with small accessory sensory structures on the tip of the second segment.

Spinneret: The spinneret resided midline between the maxillae on a line between the two palpifers. It consisted of a tapering tube-like distal fusulus and a proximal wedge-shaped basal component, the fusuliger. Fusulus and fusuliger measured 32 and 12 microns in length respectively.

Hypopharynx: The hypopharynx began as a broad flattened area anterior to the labial palps. It then continued posteriorly into the oral cavity as a smooth central trough on the floor of the mouth, flanked laterally by fleshy lobes of the paraglossae. Small tiny spines (2-3 microns) decorated the paraglossae. These spines were directed medially and often paired as doublets. No spines were observed on the hypopharynx proper.

Epipharynx: The membranous epipharynx lined the oral surface of the labrum and was covered with a dense layer of micropile. Three stout seta-like appendages (6 microns) were also found on the anterolateral margins of the oral-side labrum. These setae were directed in the general direction of the central labral notch.

Chaetotaxy of Cranium. All cranial setae of the first instar were considered to be primary setae and they persisted through subsequent instars with very little variation. They were uniformly smooth, non-spiculated, and without supporting chalazae typical of primary setae of the thorax and abdomen. Cranial setae were divided roughly into two different size groups, long and short. Long setae (tactile) were distributed evenly over the anterior parts of the head, more or less confined to those areas not normally retracted into the prothorax. Short setae (proprioceptors) were much reduced in size and number, and confined to the broad areas of the head (vertex and lateral) which easily retracted into the prothorax. Many of these setae were impossible to examine without the aid of scanning electron microscopy. Cranial punctures were also accessible to SEM study when a light coating was applied to the specimen. The reader is again referred to Figure 11 for discussion of cranial setae. Setation is described for the left half of the head capsule only; the opposite half is symmetrically identical.

Frontal (F) and Clypeal (C) Groups: The frons was open all the way to the cervical triangle and the apex of the frons was covered by cervical musculature. Frontal seta F1 was located at the base of the frons near its junction with the clypeus. F1 was relatively small and averaged 13 microns in length. A frontal puncture (Fa) was

found medial to F1 on the same level near the midline. Clypeal setae C1 and C2 were equal in length, but considerably longer (50 microns) than F1. Along with setae of the articulated mouthparts, C1 and C2 were often the only cranial setae visible when the head was retracted deeply into the prothorax (Fig. 22). C1 was located laterally near the adfrontal suture and C2 was located medially nearer the midline. A small puncture (Ca) was found midway between C1 and C2.

Adfrontal Group (AF): Closely aligned with the lateral margin of the adfrontal suture were two short setae AF1 and AF2 (8.5 microns). Both setae were located adjacent to the upper portion of the suture with AF2 dorsal to AF1. On this same line ventral to AF1 was a small puncture (AFa).

Anterior Group (A): The anterior group was comprised of two setae and a puncture. A1 was immediately above the antenna close to the mandibular condyle. A2 was located directly behind it at the level of ocelli I and II, while puncture Aa was lateral to A2 in close association with the same ocelli. A2 (23 microns) was slightly longer than A1 (17 microns).

Ocellar Group (O): A single short seta (01) was present inside the ocellar circlet near ocellus III. Puncture Ob, described as an accessory puncture by Hinton (1947), was situated anteriorly between ocelli III and IV.

Subocellar Group (SO): Seta SO2 was the longest (50 microns) of this group and occupied a position just posterior to ocellus V. SO3 was the next longest (40 microns) and was located near the basistipes on a vertical line ventral to SO2. SO1 was the smallest member of the group (25 microns) and was found immediately beneath the antennal socket next to the mandibular articulation. No less than five punctures were found in the subocellar region. The largest puncture was located beneath SO2 and was designated SOa. Remaining accessory punctures were not named.

Lateral (L) and Genal (G) Groups: The lateral region of the epicranium was completely devoid of setae and punctures. Genal seta G1 was very minute (4 microns) and the only seta found on the gena. Puncture Ga was a short distance behind and above G1.

Posterior Group (P): The posterior group consisted of a single seta (P1) found immediately posterior to the last member of the anterior group (A2). P1 was extremely small (4 microns) and somewhat closer to the adfrontal suture than A2. Puncture Pa was not located.

Vertex (V) Group: Setae of the vertex group were reduced in number and size. V1 was located lateral to AF2 and V2 was slightly posterolateral to V1. Both setae were minute (4 microns). No puncture was located.

Labrum: Six pairs of setae and a puncture were present on the anterior surface of the first instar labrum (Fig. 11C). Two of the setae were located on the flat facial surface (medial group) and the remainder were distributed along the inferior and lateral margins (lateral group). In the medial group, M1 occupied the innermost position with M3 just lateral to it. M3 was the longer of the two measuring 23 microns in length. The lateral group consisted of L1 and L2 on the true lateral margin of the labrum, plus L3 and L4 on the anterior margin projecting slightly medially. A small puncture was noted at the apex of the labral notch.

Chaetotaxy of Body. Five types of setae were found on the first instar larva. (1) Major spiculiferous setae (Fig. 13 A). These setae were generally long and measured up to 400 microns in length. They were uniformly covered with a dense cloak of

distally-projecting microspines or imbrications. Each was supported by a stout smooth cylindrical chalaza. Spiculiferous setae compromised the majority of primary setae found on the body of the first instar larva. Likewise, the numerous secondary setae of subsequent instars were also spiculiferous in type. (2) Filiform setae (Fig. 13B). These setae were very fine and hairlike in appearance. The distal tip was minimally expanded and capitate. They were confined to the prothoracic shield on all instars where they probably served a sensory function. Their base was recessed into the shield in what looked like a small circular opening (puncture). Setal size ranged from very small in the first instar (40 microns) to quite long in the fourth instar (375 microns). (3) Tufted setae (Fig. 13C). These setae were moderately long (120 microns) and appeared to be modified spiculiferous setae. They were spiculated in the normal fashion proximally, but the distal third was decorated with a dense tuft of spines twice the size of proximal spiculations. Tufted setae were found only on the suranal fold of the tenth abdominal segment where they projected backwardly over the anal opening. Each was borne on a stout smooth chalaza. (4) Thorny setae (Fig. 13D). These setae were medium-sized in length (60 microns) and appeared to be a modification of smooth non-spiculated type setae. Immediately after emerging from their chalaza, they branched into multiple thornlike spines. Spines projected upwardly and outwardly from the central setal stem. Secondary branching was not noticed. These setae were located on the subanal fold of the last abdominal segment and formed part of a continuous row of subanal setae that swept under the anal opening. (5) Smooth non-spiculated setae (Fig. 13E). These setae were indistinguishable from cranial setae except for the cylindrical chalaza that supported them. Chalazae were absent on the cranium. Smooth setae varied considerably in size and accordingly were divided into two functional groups. They reached 60 microns in size in the subventral area and subanal fold where they most likely served a tactile function. On the other hand, they were truly microscopic in size (2-10 microns) on the venter and intersegmental grooves where they undoubtably functioned as proprioceptors supplying information about body movement and position. Finally, it is also probable that some medium-sized smooth setae (30 microns) functioned as proprioceptors for specialized areas of the body like the ventral prolegs.

Lenticles were also prominent features of the larval integument (Figs. 13F & 28). Their characteristic shape included a circular cone-shaped side wall which was smooth and heavily sclerotized. The pimple-like dome covering on the top of each lenticle was membranous and non-sclerotized. Perforations in the dome were not appreciated in first and second instars, but they were readily discernible in later instars. Lenticles averaged about 15 microns in height, 30 microns in width at the base, and 17 microns wide at the dome. While not derived from setal origins, they were distributed in an orderly arrangement on first instars and therefore were mapped along with setae in preparation of Figure 12. Lenticles were more or less aligned in horizontal rows in the following regions: subdorsal (SDL), supraspiracular (SSL), and subventral (SVL).

The highly-modified structures seen in Figures 13G and 13H were specialized setae confined to later stages (fourth instar and pupa). They were quite unique to *Lycaena* and apparently restricted to this group. They will be discussed separately below with their corresponding developmental stage.

In following the discussion of specific arrangement of first instar setae and

lenticles, the reader is advised to refer to the setal map in Figure 12. In this figure, only structures on the left side of each segment were depicted and described. From time to time, additional reference is made to specific SEM photomicrographs to further aid the discussion.

Prothorax and Prothoracic Shield: The prothoracic shield was well-sclerotized and resided on the dorsum of the prothorax (Figs. 13I and 23). It consisted of two flat circular plates joined together roughly in the shape of a figure "8". A larger circular plate (130 microns) was located posteriorly and a smaller plate (60 microns) anteriorly. Four pairs of setae and a pair of lenticles were found on the shield. A major spiculiferous seta (D2) resided on the anterior margin of the anterior plate near the midline. A small apical projection of the shield separated the bases of the paired D2 setae. Just posterior and slightly lateral to D2 was a lenticle and immediately posterolateral to the lenticle was another major spiculiferous seta (SD2). This completed the complement of setae and lenticles on the anterior plate. The posterior plate had a major siculiferous seta (SD1) on its anterior margin on a line directly posterior from the lenticle of the anterior plate. SD1 was the longest seta (200 microns) of the entire shield; the other major setae were only about two-thirds as long. Posterolateral to SD1 and situated near the lateral margin of the posterior plate was a very fine filiform seta (XD2) which originated from a depressed puncture-like circular opening. XD2 averaged 40 microns in length and had a slightly clubbed distal tip.

Except for XD2, all setae of the shield attained considerable length and projected anteriorly over the head and neck in a dangling fashion. These setae formed part of a continuous series of setae on the anterior prothorax that coursed around the front of the larva as a setal fringe. On the sides of the larva, the anterior setal fringe joined with lateral setae to create an effective skirt of setae around the entire larva. On the prothorax lateral to the shield, four major spiculiferous setae comprised the remainder of the anterior fringe. These setae formed a diagonal line parallel to the anterolateral margin of the prothorax. The most medial of the four setae (MD1) was the shortest (120 microns) and approximately equal in size to D2 on the front of the shield. Posterolateral to MD1 on the same diagonal line was MSD1 (200 microns). MSD2 (170 microns) and L1 (170 microns) were the remaining setae of this diagonal group. The majority of the anterior fringe setae, especially shield setae and MD1, projected forwardly over the head and seemed to protect the retractable portion of the head which contained only tiny microscopic setae.

Two other setae of the lateral group, L2 (100 microns) and L3 (170 microns), were located close together on the lateral body fold of the prothorax, immediately beneath L1 and anterior to the small prothoracic spiracle. In the subventral area beneath the body fold were two additional very small setae (SV1 and SV2) and a lenticle. The larger SV1 (100 microns) was spiculiferous, while the smaller SV2 (30 microns) was non-spiculiferous and placed anterior to SV1. The lenticle was placed immediately above both setae. Downey (1979) referred to lenticles beneath the lateral setae as sublateral lenticles, but I prefer to designate them as subventral lenticles keeping with the terminology of the SV setal group to which they are closely associated.

Mesothorax: Striking double rows of major spiculiferous dorsal setae began on the mesothorax (Fig. 21) and continued posteriorly onto abdominal segments. These setae were the largest found on the body of the first instar and they formed a

conspicuous part of the lateral body profile. D1 was medial in position and located adjacent to the mid-dorsal line. Supported by a large chalaza, D1 projected a gradual curve that moved upward, then backward and a little outward. D2 began slightly posterolateral to D1 and projected upward and strongly backward without any outward flare. On the mesothorax, D1 measured 420 microns in length and D2 nearly the same (400 microns). On subsequent segments, D2 became substantially shorter than D1.

On the extreme anterior margin of the mesothorax near the intersegmental groove (Fig. 21), there was a tiny microscopic seta (MD1). This seta averaged two microns in length and was usually located in the subdorsal region just anterior to the subdorsal lenticle. Its location near the intersegmental groove on all segments from the mesothorax to the ninth abdominal segment would indicate a proprioceptor function. The subdorsal lenticle of the mesothorax was uniformly present in all larvae examined and initiated a distinct row of subdorsal lenticles that continued to the seventh abdominal segment.

Lateral setae were all spiculiferous and formed a straight horizontal line on the lateral body fold (ridge). These setae were equidistant apart and designated L2, L3, and L1 from cephalad to caudad. The middle seta L3 was routinely the longest averaging 180 microns in length. The cephalad seta L2 was the next longest (160 microns) and the caudad seta L1 was shortest (110 microns). These respective lengths apply not only to the mesothorax, but also to the metathorax and abdominal segments one through seven. When viewed from above, each lateral seta was observed to project a slight gradual curve toward the rear of the larva. This curve was more pronounced on abdominal segments.

Beneath the lateral ridge in the subventral area, setae SV1 and SV2 and a small lenticle were found in a straight line. As on the prothorax, SV1 was larger and spiculiferous, while SV2 was non-spiculiferous and placed anterior to SV1.

Metathorax: The setal pattern of the metathorax was identical to that of the mesothorax in all respects. MD1, D1 and D2, subdorsal lenticle, L1, L2, L3, SV1 and SV2, and a subventral lenticle were all present. Setal lengths were also identical except for a minor shortening of D1 (400 microns) and a significant shortening of D2 (280 microns). These relative lengths remained essentially unchanged for the remainder of the segments which had setae of the dorsal group.

Abdomen: First Segment (A-1): MD1, D1 and D2, subdorsal lenticle, L1, L2, L3, and SV1 were present. SV1 on A-1 and remaining abdominal segments was now non-spiculiferous and considerably shorter (60 microns) than SV1 of the thorax. SV2 and the subventral lenticle were absent. On the venter, a small microscopic seta MV3 (10-12 microns) was found adjacent to the mid-ventral line. Hinton (1946) described as many as three microscopic proprioceptors occurring on the venter of first instars with MV3 being the most ventral and the only one present on abdominal segments. Spiracles were present in a continuous line on segments A-1 through A-8. Each spiracle was placed slightly anterior to the midpoint of each segment.

Second Segment (A-2): MD1, D1 and D2, subdorsal lenticle, L1, L2, L3, and SV1 were present. The venter contained a microscopic MV3 near the midline, plus an additional larger non-spiculiferous seta V1 (45 microns) just lateral to MV3. This medium-sized seta seemed to fill the gap on the bottom of the larva between the last pair of thoracic legs (metathorax) and the first pair of ventral prolegs (A-3). In this

position V1 could serve either a tactile or proprioceptor role. A new lenticle appeared on this segment in the supraspiracular region. It was located nearly equidistant between the spiracle and the subdorsal lenticle, on occasion being slightly closer to the latter. The A-2 supraspiracular lenticle was absent in one larva.

Third to Sixth Segment (A-3 to A-6): MV1, D1, and D2, subdorsal and supraspiracular lenticles, L1, L2, L3, SV1, and MV3 were present. A small subventral lenticle was also present on A-5 and A-6, just anterodorsal to SV1. Each ventral proleg bore two ventrolaterally-projecting smooth non-spiculiferous setae. The anterior proleg seta was somewhat smaller (30 microns) than the posterior seta (45 microns). It would appear that these setae served a proprioceptor role since they made contact with other prolegs and adjacent substrate during movement of the legs.

Seventh Segment (A-7): MD1, D1, subdorsal lenticle, L1, L2, L3, SV1, and SV2, and MV3 were present. A number of changes in the pattern of the dorsal region were appreciated in this segment. D2 dropped out and was replaced by a dorsal lenticle on the posterior half of the segment. Also D1 and the subdorsal lenticle migrated slightly posteriorly. (An alternative interpretation would find the subdorsal lenticle having migrated to the position of the absent D2 and the supraspiracular lenticle in turn having migrated to the subdorsal region.) Both SV1 and SV2 were non-spiculiferous. On this segment, SV2 was located anterodorsal to SV1 instead of on a straight line as was seen in thoracic segments.

Eighth Segment (A-8): MD1, D1, L1, L2, L3, SV1, and MV3 were present. D2 was absent and no lenticles were present. The lateral setae were present in the standard configuration, but the posterior seta L1 was reduced in size (80 microns).

Ninth Segment (A-9): A narrow but distinct ninth abdominal segment was present and separated from the tenth segment by a visible intersegmental cleft (Fig. 24). This contrasted with the finding in some lycaenids (Plebejinae) where the two terminal segments were apparently fused. MD1, D1, L1, SV1, and MV3 were present on the narrow ninth segment. No lenticles were seen. Due to the size of the segment, the lateral series was reduced to a single seta, L1 (140 microns). Hinton (1946) designated the solitary A-9 lateral seta as L1.

Tenth Segment (A-10) and Anal Shield: A broad mid-dorsal anal shield was present. It was saddle-like in shape (220 x 110 microns) with the anterior portion parallel to the intersegmental cleft and the posterior portion rounded to fit into the terminal contour of the segment. Lateral poles of the shield were densely sclerotized and contained two side-by-side lenticles (Fig. 24). The central portion of the shield was minimally sclerotized, almost imperceptibly so. This created in some larvae the false appearance of two separate shields. No setae were found on the shield.

Three major spiculiferous setae were present on the lateral ridge of the last segment and appeared to be continuous with the lateral series of previous abdominal segments. Following the same convention used on other segments, these setae were designated L2, L3, and L1. Their respective lengths were 150, 200, and 250 microns. A pair of tufted setae was found on the suranal fold on a line slightly ventral to the spiculiferous lateral setae but still dorsal to the anal slit. They were somewhat shorter (120 microns) than lateral setae and their terminal tufts dangled posteriorly directly behind the anal opening. One of these tufted setae was medial to L1, resting next to the mid-dorsal line. The second was lateral to L1 and equidistant

between L1 and L3. Hinton (1946) did not discuss setae of A-10, and the exact nature of the tufted setae is therefore quite speculative. (See discussion). For purposes of this study, tufted setae were simply described and left unlabeled.

The integument of the suranal and subanal folds was covered with a dense coat of epicuticular microspines (Fig. 24). These spines were directed posteriorly and averaged 15 microns in length, nearly seven times longer than the tubercles regularly found on the rest of the body. They were derived directly from the epicuticle and did not have separate chalazae or pinacula. On the suranal fold, integument spines covered the entire fold and advanced to the upper margin of the anal slit. On the opposite side of the slit, the dorsal portion of the subanal fold was completely spineless and marked with a series of very shallow longitudinal grooves. These grooves coursed caudoventrally for a distance of approximately 30 microns before being replaced by spines which covered the remainder of the subanal fold. The subanal fold also supported a horizontal row of continuous small setae that originated on the lateral portion of the anal proleg and then swept medially beneath the anal slit. This series consisted of six setae: four microsetae and two thorny setae. It was judged that all were derived from the anal proleg and comprised a unique anal proleg setal group. The first and most anterior of this series was a typical smooth microseta on the lateral aspect of the anal proleg. Second in line and immediately posterior to this was a thorny seta. Although these two setae were laterally-placed, they were not considered to be constituents of the subventral group. (See discussion.) These setae rested on a line below the subventral position of cephalad segments and they projected more posteriorly than laterally. Modification of the second seta clearly suggested its association with other thorny setae of this series. Following the second seta, the horizontal series continued around the postero-lateral margin of the proleg where a typical microseta was next in line. This was followed medially by another thorny seta which was slightly larger than the first. Finally, two more medial microsetae finished the series at the midline. (Two additional microsetae, not part of the subanal series, were located on the anteromedial portion of the anal proleg.) Right and left anal prolegs were bilaterally symmetrical. The subanal series of both prolegs together effectively formed a continuous uninterrupted series around the rear of the larva.

Prolegs. Crochets of the first instar ventral prolegs were arranged in a uniordinal mesoseries of eight crochets interrupted by a fleshy spatulate lobe (Fig. 13 M). The mesoseries was very strongly curved in a form of a mesopenellipse and separated into anterior and posterior groups of four crochets each. The anal proleg also had eight crochets, but interrupted into groups of six and two. The group of two was located posteromedially, while the group of six formed a series that swept anteromedial to anterolateral around the front of the anal proleg.

SECOND INSTAR

General. The second instar maintained an onisciform shape (Figs. 4 & 26) and measured 2.5 mm in length immediately following the first molt and 5.0 mm in length just before the second molt. Head capsule width averaged .390 mm. The body was green in color with semi-glossy texture and a stripe pattern similar to the first instar (Fig. 4). A bold dorsal red stripe ran in the dorsal midline from the mesothorax to A-10 and was bordered on both sides by a solitary subdorsal white stripe. Ventral to this was a faint double row of oblique white dashes (two per

segment) which slanted at a 30° angle oriented anterodorsal-posteroventral. On the lateral side of some larvae, there was an extra faint white line of broken horizontal dashes at the level of the spiracles. Finally, all larvae had a bold white stripe on the lateral ridge. The above description represents the fully-developed typical color pattern, but minor variations from one larva to another were common. Patterns of variation most often involved reduction in size of the dorsal red stripe, which was often restricted to the last few abdominal segments only, and reduction in intensity of the subdorsal oblique white dashes. An uncommon variant lacked red and white stripes except for the white line on the lateral ridge, leaving virtually a solid green larva. The color of the spiracles, chalazae, and lenticles was brown as before and the head capsule was very dark brown, nearly black.

Integument. A radical change occurred in the microanatomy of the integument between the first and second instar. The entire surface of the integument was now highly sculptured and organized into a distinctive pattern (Fig. 31). This pattern consisted of uniformly-spaced oval depressions dispersed over the epicuticular surface. Each oval contained a small hole in its center. The epicuticle surrounding each oval was non-depressed and in effect became an "elevated" ridge separating adjacent ovals. The typical oval depression averaged 15 microns in length, 10 microns in width, and 3 microns in depth. The central hole averaged 3 microns in diameter. This basic pattern of depressed oval integumental units was maintained in the remaining instars.

The geometrical pattern of large pits in the integument was identical to that of the first instar when compared segment by segment (Figs. 26 & 30). However, an additional feature that appeared in the second instar was the presence of furrows. Furrows were nothing more than simple folds in the integument and often originated near structures routinely depressed in the integument (e.g. prothoracic shield, integument pits). The only substantial furrow of note was a large one that began at the lateral wing (ala) of the depressed prothoracic shield and swept posteriorly through the prothorax, mesothorax, and metathorax at the subdorsal level (Fig. 27).

Chaetotaxy of Body. The addition of secondary setae to the larval body following the first instar dominated the chaetotaxy of the second and subsequent instars. Numerous secondary setae (25-30/segment) of the major spiculiferous type were now scattered over the body and, as a result, second instar larvae appeared quite "hairy" (Figs. 26 & 27). The pattern of primary setation from the first instar was now nearly obscured. The number of lenticles was likewise amplified and distributed irregularly over the body surface. Large primary setae of the dorsal group (D1 & D2) and lateral group (L1-3) could be picked out with some difficulty, but all other primary setae were unrecognizable. In the face of such huge numbers of secondary setae and additional lenticles, setal maps of second and subsequent instars were deemed useless. Only the prothoracic shield was spared invasion by secondary setae and may therefore prove important for comparative taxonomic studies. Like the integument pattern, the shape of the prothoracic shield changed radically between the first and second instar (Figs. 13J & 29). When viewed from above, the second instar shield was elongate (230 microns) and supported two separate pairs of lateral wings (alae). The anterior alae were longer, thinner, and more sharply pointed than the short and rounded posterior alae. Width of the shield at the anterior alae was 270 microns and width at the posterior alae was 120

microns. Anterior alar width was slightly greater than the axial length of the entire shield. Two pairs of primary setae were present on the alar arms. The filiform XD2 was situated on a button-like chalaza in a circular depression on the anterior alae. It was considerably longer (150 microns) than the first instar XD2 (40 microns). A pair of spiculiferous primary setae (SD1) was located on the posterior alae and measured nearly the same size (210 microns) as SD1 on the first instar shield. The lenticle seen in the upper portion of Figure 29 was associated with adjacent integument and did not reside on the shield proper.

Cranial setae and internal sculpturing of the spiracles were not studied in this instar.

THIRD INSTAR

General. The third instar was onisciform in shape (Figs. 5 & 32) and measured 5.0 mm at the beginning of the instar and 8.0 mm at the end. Width of the head capsule averaged .632 mm. Body color was green with a distinct matt appearance and the stripe pattern was less striking than in previous instars (Fig. 5). A reduced and very faint red dorsal stripe occurred on the dorsal midline from the first to the eighth abdominal segment. This stripe was bordered on both sides by a faint white subdorsal stripe. In some individuals, both dorsal and subdorsal stripes were completely absent. Finally, a white stripe on the lateral ridge was uniformly present. This stripe was present in all instars, including those with variations in stripe pattern. The color of the spiracles, chalazae, lenticles, and head capsule was as before.

Integument. The basic pattern of depressed oval units was the same as in the previous instar (Figs. 36 & 31). One modification occurred. Epicuticular ridges situated between the oval depressions now supported very thin vertical partitions of chitinous material. These partitions averaged 3.5 microns in height and gave the integument a "honeycombed" or "chambered" appearance. This type of surface topography greatly reduced spectral reflectance.

The geometrical pattern of large integument pits (Figs. 33 & 36) was again the same as in the previous instars. Function of these pits was unknown and they seemed to show virtually no change from one instar to the next. Lastly, a large furrow in the integument was again found beginning at the anterior ala of the depressed prothoracic shield and curving posteriorly through the prothoracic segment.

Spiracles. Internal sculpturing of the spiracles (Fig. 34) differed significantly from the first instar. On the inside of the spiracular opening, flattened coral-like lobes of chitin extended parallel with spiracular walls for a short distance before terminating at the junction with endotrachea. Each flattened lobe resembled the palm of an extended hand bearing small spiny fingers. These fingerlike processes interconnected freely with adjacent lobes.

Chaetotaxy of Body. Secondary setation was amplified to 130-140 setae per segment. The larval body was extensively covered with spiculiferous secondary setae (Figs. 32 & 33) over the entire body except for the prothoracic shield, intersegmental clefts, and the venter. All setae were nearly uniform in size (300 microns) and the primary setal pattern was now totally lost. In relationship to total body size, body setae were now comparatively smaller than in previous instars.

Within the multisetose pattern, large numbers of lenticles were also scattered randomly over the body surface.

The prothoracic shield had the same configuration as that of the second instar (Figs 13K & 35). The shield measured 400 microns in length, 320 microns in width at the anterior alae, and 120 microns in width at the posterior alae. Filiform seta XD2 measured 230 microns and was again situated on a small button-like chalaza in a circular depression on the anterior alae. A pair of spiculiferous setae (160 microns) routinely appeared on the posterior half of the shield, but they were rarely arranged in a symmetrical position. They may have represented asymmetric SD1 setae, but it is also quite likely that they were random secondary setae that invaded the shield. Random unpaired lenticles were a frequent finding on the shield.

FOURTH INSTAR

General. The fourth instar was onisciform in shape, and appeared to have a much broader prothoracic segment (Figs. 6 & 38). The widened lateral portions of the prothorax were frequently noticed wrapped around the head capsule and food substrate. This instar measured 8.0 mm at the beginning and 15.0 mm before entering prepupal quiescence. Just prior to pupating, the prepupal larva contracted considerably in length (9.0 mm) and rounded-up to form a broad axial arch (Fig. 7). The head capsule width averaged 1.05 mm. Body color was green with a distinct matt appearance similar to the third instar. On the whole, no stripes were present on the upper surface of the body and the solid green larva blended nicely with its foodplant. A dark green haemolymph vessel could be seen beneath the integument in the dorsal midline with exceptional larvae showing an extremely faint subdorsal white line bordering this haemolymph vessel. The lateral ridge uniformly contained a continuous white line, more often than not on the underside of the ridge (body fold) and not visible when viewed from the side. Color of the sclerotized parts (head capsule, chalazae, lenticles, spiracles) was as in previous instars. Spiracles in this instar were considerably bigger than before and demonstrated a brilliant white center surrounded by a brown spiracular ring.

Integument. The basic surface pattern was as in the previous instar except partitions between depressed units were now twice as high (8 microns). This greatly enhanced the "honeycombed" appearance of the integument (Fig. 43). When viewed directly from above, each surface unit delineated by the partitions appeared to have six sides. The tops of these partitions were wrinkled and wavy in nature and it was very difficult to observe into the depths of each unit because of the height of the partitions. Surface honeycombing effectively reduced spectral reflectance.

The geometrical pattern of large conical pits in the integument remained constant in this instar and throughout development. Although these pits showed essentially no change in position, they were significantly wider and structures at the bottom of the pits could now be visualized. Pits extended to a depth of 60-70 microns and their sides were covered with honeycombed integument. Each pit terminated with a round slightly convex button (20 microns) that occupied the floor of the pit. This button-like structure resembled some form of sensory placode. Its likely association with fixed segmental innervation may account for the invariable geometrical pattern of integument pits.

Integument furrows were now less evident on the prothorax since the shield was depressed to a much lesser degree into the integument.

Spiracles. Spiracles (Fig. 40) were very large (50 microns) and round. Internal sculpturing was elaborate and nearly filled the lumen leaving only a vertical slit-like opening (15 x 3 microns) in the center of the spiracle (Fig. 41). Detailed sculpturing was built upon the lobar pattern of the previous instar, but in this instance it was even more highly-branched and coral-like (staghorn coral). The chitinous meshwork was pure white in color.

Chaetotaxy of Cranium. Chaetotaxy of the fourth instar head capsule showed persistence of the primary cranial setal pattern with the addition of only a few new secondary setae. Very little new information was gained. Setation of the frontal, clypeal, adfrontal, genal, posterior, and vertex groups remained essentially unchanged from the first instar. The anterior group had added three new small microsetae in a vertical straight line medial to A1. The ocellar group was the most noticeably changed and a total of 14 microsetae now comprised this complex. As in the first instar, no seta was found anterior to the ocellar circlet, but six microsetae were now present within the circlet itself. One of these was presumed to be 01. A second group of eight microsetae occurred immediately posterior to the ocellar circlet, and one seta closely situated behind the sixth ocellus was slightly longer and presumed to be 02. There was a great deal of intraspecific variability within the ocellar complex. Some individuals did not even have the same number of ocellar setae on the two opposite halves of the cranial capsule. In the subocellar group, primary setae S01, S02, and S03 were still in an identical position to the first instar pattern. S03 was now a little longer. A new small microseta appeared between S01 and S03, plus another new microseta appeared immediately behind S03, making a total of five subocellar setae.

The labrum (Fig. 11 E) measured 420 microns in width and now had four pairs of setae in the medial group (M1-4) with M3 still being the longest (100 microns). Lateral group setae (L1-4) were nearly equal in size except for L2 on the anterolateral margin which was comparatively lengthened (50 microns) and measured approximately twice the size of other setae of the lateral group. The small puncture that was located in the first instar labral notch was not present in this instar.

The mandible (Fig. 11 F) measured 280 microns in length and now possessed a new type of biting edge. On the anterior margin of the occlusal plane, there were three small rounded incising teeth followed by a long knife-like cutting edge with fine serrations. This edge terminated laterally with a knob-like tooth. Two setae projected from the posterolateral mandibular margin.

Head capsule dehiscence occurred by cleavage along the adrontal sutures beginning at the cervical triangle and extending to the base of the mandibular insertion. Following this, the two epicranial halves rotated outwardly in the fashion of an opening book, thus creating a large dorsal exit hole.

Chaetotaxy of Body. Secondary setae of the spiculiferous type reached absolutely massive numbers on the body giving the larva a very dense "hairy" appearance (Figs. 6 & 38). Approximately 350 to 400 setae of this type were found on each segment. They uniformly averaged 250 microns in length and were comparatively shorter than their counterparts on the second and third instar. Numerous randomly arranged lenticles were also present. The primary setal pattern of the body was again totally obscured and dominated by secondary

setosity. In fact, one wondered if primary setae truly even existed at this stage of development. Recognizable primary setae were limited to the head capsule and prothoracic shield.

A new element appeared on the body of the fourth instar. This was a specialized form of secondary seta resembling a tiny "mushroom" (Figs. 13 G & 42). These setae numbered approximately 100 per segment and were much smaller than spiculiferous secondary setae. Because of their dwarfed size and random distribution over the integument, they brought to mind a vision of "mushrooms in a forest". Individually, they ranged from 55 to 65 microns in height and averaged 34 microns in diameter. Each was borne on a separate chalaza and had approximately 50 thin blunt-tipped lobes projecting from the distal half. Collectively, the lobes projected upward and outward and gave the seta a globular contour. These setae were uniquely restricted to the integument of the last (fourth) instar.

The prothoracic shield maintained the same double-winged contour as seen in the second and third instar (Figs. 13 L & 39). The shield measured 540 microns in length, 400 microns in width at the anterior alae, and 170 microns in width at the posterior alae. In this instar, anterior alae were considerably broadened at their bases and merged together at the apex of the shield. When viewed from above, the shield resembled a large arrow pointing cephalad. Filiform seta XD2 (375 microns) was situated on a button-like chalaza in a circular depression at the lateral extremes of the anterior alae. Two or more asymmetric pairs of spiculiferous secondary setae and occasional lenticles often invaded the shield.

Prolegs. Crochets of the ventral proleg (Fig. 13N) were still arranged in an interrupted mesoseries, but with considerably more crochets than the first instar. The medial surface of each proleg contained approximately 60-70 crochets interrupted into two distinct groups (anterior and posterior) by a central spatulate lobe. Each crochet group had a multiseries of nine to ten rows of near equal-sized crochets. Such an arrangement was designated an interrupted mesomultiseries. On the lateral aspect of each proleg was a uniordinal lateroseries of five crochets alligned in a straight horizontal row. This lateroseries was not present in the first instar.

PUPA

General. The obtect pupa of *L. epixanthe* was very short and plump in profile (Fig. 8). Length averaged 8.5 mm and ranged from 7.6 to 9.0 mm. Viewed from above, sides of the wing cases were straight except for a slight divergence at A-4 where the greatest width occurred (4.0 mm). Posteriorly, the abdomen was elliptical and well-rounded. Anteriorly, the thorax tapered very slightly in front of the wing bases, but terminated sharply truncate at the extreme front end of the pupa. Viewed from the side, the pupa looked double-humped. The abdomen was strongly arched and evenly rounded and reached a maximum height at A-4 (3.8 mm). The tiny last segment of the abdomen dropped off nearly perpendicular to the ventral surface which was flat throughout its entire length. A second prominent hump appeared on the mesothorax (3.5 mm) which was only slightly shorter than the abdominal hump at A-4. Anteriorly, the thorax sloped rapidly to the front of the pupa, while posteriorly the thoracic slope was gentle and formed a shallow curve at the point of junction with the abdomen. The head and cranial appendages were located on the ventral surface of the pupa as was a small semicircle of minute cremastral hooklets

looped around the anal slit.

Immediately following the fourth molt, the great majority of pupae were uniformly solid green in color. Within a few hours, dark maculations had developed (Fig. 8). These maculations were organized more or less in series of longitudinal rows starting on the mid-dorsum where a fine black line extended from the prothorax to tenth abdominal segment. This line was punctuated by dark black maculations (one per segment) which were somewhat larger on abdominal segments. Lateral to the mid-dorsal line was a very faint, nearly obscure subdorsal row of brownish dots (one per segment). Below this was a supra-stigmatal row of dark black macules (2-3 per segment) beginning on the mesothorax and extending posteriorly. Finally, three more rows of weak black macules (one per segment) completed the maculation pattern. These rows occurred respectively in a line with abdominal spiracles, in a substigmatal row, and in a subventral row. The spiracles were colored pure white centrally and ringed with light brown. After five to six days, the wing cases became cream-colored and infuscated with light brown streaks. Eye, proboscis, and antennal cases were also infuscated with brown. Approximately, two days before eclosion, eye cases became dark black. The following day the thorax and abdomen also blackened. On the day of eclosion, the pupal skin was completely transparent and the imago visible beneath. Emergence of the adult was accomplished by a mid-dorsal split of the thoracic segments.

Approximately five percent of the pupae were uniform blackish-purple in color (deep wine color) without any trace of green or maculations. This was an unexpected polymorphism in pupal color. The purple morph demonstrated no detectable ultrastructural differences when compared with "typical" green pupae. Likewise, adults derived from the purple pupae showed no differentiating features.

Integument. The integument surface was covered with a fine reticulation of small elevated lines or ribs. These ribs varied in height from four to five microns and looked like fine delicate tracery when viewed on low magnification (Fig. 44). The rib network followed irregular courses and intersected frequently. At points of intersection, small doughnut-like papillae with plugged central pits interrupted the narrow ribs (Fig. 45). Integument between the ribs was divided into large angular polygons which contained numerous sensory verrucae and a specialized seta unique to the pupa (Fig. 45). (See chaetotaxy below). The sensory verrucae bore some resemblance to larval lenticles. They measured 15-20 microns in diameter and eight microns in height. Each had a circular exterior wall with a central dome-shaped membrane. A distinct groove separated the exterior wall from the central dome. These verrucae were heavily clustered around spiracles where ribbing was absent (Fig. 46).

Spiracles. The chitinous internal sculpturing of the spiracles was highly elaborate and coral-like, but quite unlike that seen in the larval instars (Fig. 47). Spiracular openings measured five microns in diameter and from their inner walls arose bluntly-rounded spatulate projections (15 x 5 microns) bearing fine chitinous spines. The lobulated sculpturing was white in color and filled the spiracular opening leaving only a vertical slit-like space communicating with the deeper tracheal system.

Stridulatory Organ. A well-developed stridulatory organ was located on the dorsal intersegmental membrane between the fifth and sixth abdominal segments and extended laterally to the level of the spiracles. The organ consisted of an

opposing file and grating plate with a deep intersegmental cleft between (Fig. 48). The stridulating plate itself was located on the dorsal posterior membrane of A-5 and consisted of a narrow sclerotized band approximately 50 microns in width. The plate was characterized by small knob-like tubercles (2-3 microns in height) situated on fine transverse reticulations. The tubercles were aligned in loose transverse rows upon these reticulations. The file was located on the opposing anterior portion of A-6 and readily identified by its conspicuous sharp teeth. The recurved teeth were regularly spaced and easily imagined to grate against the opposing plate on A-5. Horizontal reticulations were also present on the file. A deep cleft representing the intersegmental fold plunged between the plate and file. Additional small tubercles and teeth, similar to those of the stridulatory organ, were also found loosely scattered on other intersegmental membranes of the abdomen not involved with sound production.

Chaetotaxy. A specialized trumpet-shaped seta, unique to the pupa, was found within the angulate polygons of the pupal integument (Figs. 13H & 49). This seta was present over the entire body surface except for the wing, head, and cranial appendage cases. It was present on the venter, but numbers were somewhat reduced there. No useful taxonomic arrangement was detected in their placement and, to the naked eye, they appeared as dainty white pubescence. Individually, each seta measured 35 microns in height and terminated in an infundibular disc (funnel-shaped) averaging 40 microns in diameter. The disc was decorated with 15-20 small spines projecting from its peripheral margin. A few additional spines were located on the dorsal surface within the shallow "funnel". The base of the seta inserted in a central socket of a small cone-shaped pinaculum.

DISCUSSION

Superficially, *L. epixanthe* would appear to be unique in comparison to all other species of North American *Lycaena*. This first-glance interpretation could be supported by its popularly known attributes of diminuitive size, unique habitat, and unusual foodplant. Indeed, it is the smallest of all Nearctic *Lycaena* and one of the few endemic butterflies solely restricted to bog habitats and the only butterfly utilizing cranberry. These features alone are totally unlike those of any other *Lycaena* and in this respect provide fascinating topics for study in evolutionary biology. Nevertheless, *epixanthe* remains an integral part of the lycaenine group. I found many close developmental and behavioral similarities between *epixanthe* and those published for other *Lycaena*. In many instances, generic homogeneity was striking and differences quite minor. It would appear that basic patterns of behavior and developmental morphology have been conserved within the genus.

Ecological factors that dictate the nature of bogs are both decisive for the occurrence of *epixanthe* and limit its distribution. The most important factor, of course, is the favorable environment for the growth of cranberry. The biology of the butterfly so closely parallels that of the foodplant that it is presumed that *epixanthe* is highly, or totally, restricted in its larval

foodplant preference. Oviposition and successful rearing to date have occurred only on the diploid large cranberry *Vaccinium macrocarpon*, but it is suspected that the tetraploid small cranberry *Vaccinium oxycoccos* can also serve as a foodplant. This is especially true at the northern extent of the butterfly's range in the Canadian zone where *V. oxycoccos* replaces *V. macrocarpon* as the dominant cranberry species. In many instances, *V. oxycoccos* is the only cranberry species recorded in bogs where *epixanthe* has been taken (Bird, 1956; Masters, 1968; Maddox and Cannell, 1983). Broad areas of overlap also occur in the distribution of the two cranberry species, and it is possible the butterfly will be found to use both species locally or perhaps favor the more abundant one. To test the current understanding of *epixanthe*'s exclusive association with cranberry, rearing studies involving *V. oxycoccos* and several other members of the Ericaceae are being conducted.

Year after year, emergence of adult butterflies is timed to coincide with the cranberry flowering period. Adults are weak fliers and are seldom seen far from the plant. The hostplant is clearly the major nectar resource and *epixanthe* nectars almost exclusively on cranberry blossoms. On occasion, they also imbibe dew drops from the sphagnum surface and sedge blades, but it is the strong attraction for nectar that must account in part for the butterfly's constant presence around the foodplant. Nectaring on the larval foodplant may serve to not only replenish fluid losses, but also concentrate the population and facilitate courtship and pairing during the relatively short flightperiod.

Courtship is very similar among many species of *Lycaena*. As a generalization, perching behavior is the main method of mate-locating used by Nearctic male *Lycaena* (Scott, 1975). *Epixanthe* males perch on cranberry vines from which they fly out to investigate passing objects. Successful encounters are frequent since the butterfly population is densely concentrated and confined to the limits of the cranberry substrate within the bog. From time to time, flying males may encounter females in flight, but this would appear to be more accidental than intended patrolling behavior. Females mate shortly after emergence and mate thereafter infrequently. Most successful copulations occur in the mid-afternoon during peak male perching activity. The "rejection signal" utilized by unreceptive females of *L. arota* (Scott, 1974) and *L. xanthoides* (Scott and Opler, 1974) is also used by *epixanthe* females.

Dorsal wing surfaces of male *epixanthe* reflect brilliantly in the ultraviolet range. Since insect vision includes receptors in the ultraviolet spectrum, it is strongy suspected that UV reflectance is used by adult butterflies in intraspecific sexual communication. UV reflectance is the direct result of structural interference in specialized wing scales of the discal regions. Patterns of male reflectance are very similar among all *Lycaena* (Scott, 1973; Ferris, 1977). As perching males fly out to investigate passing

females and vibrate their wings during courting, sex identification would seem unmistakable. The strongly reflective surfaces of the male wings could be likened to a beacon of light flashing "on" and "off".

The yellow/gray polymorphism for ventral wing color in the New Jersey populations appears to have no significance for sexual communication. Yellow is the most frequent (95%) color and also the type color for the species. The ventral yellow color loans its Greek derivative (*xanthos*=yellow) to the scientific name. Ventral gray color is the chief taxonomic character and distinguishing feature of the midwestern subspecies *L. e. michiganensis* (Rawson). The New Jersey low frequency (5%) gray morph is indistinguishable from the *michiganensis* holotype and a long series of the same subspecies examined at the U.S.N.M. Rawson (1948) was the first to recognize the rare New Jersey gray specimens, but he believed they were "aberrants" that appeared only periodically. In the author's study, the gray morph appeared routinely year after year, implying a balanced polymorphism. If this polymorphism proves to be genetically-controlled, as is likely, it may be important in establishing relationships between *epixanthe* subspecies and in determining sequences of post-glacial events.

Female *epixanthe* exhibit a unique technique when locating plants for oviposition. Uniformly, they select plants obscured by sedges around the perimeter of the bog or on hummocks within the center of the bog. After landing on the sedges, they walk down and through the sedge tangles to reach cranberry plants hidden below at sites they would be unable to fly to directly. Cook and Watson (1908) similarly noted that females are "almost out of site among the vines" when ovipositing.

Fecundity is a key factor to evolutionary success. Fresh-caught *epixanthe* females yield on the average 28 ova/female in confinement. This is slightly greater than the number found by Newcomb (1909) for the closely-related congener *L. dorcas* (11.5-21 ova/female). Egg production in confinement obviously depends among other things on the method and conditions of confinement and the ages of females confined. Cook and Watson (1908) reported on two *epixanthe* females which yielded 40 and 42 ova respectively when confined immediately after mating, probably reflecting a more accurate representation of the total egg numbers capable of being produced. Some isolated bogs in upland New York have *epixanthe* populations estimated to contain as few as 50-100 adult individuals per yearly generation (Shapiro, 1974). Using these figures as an example, if 100 adults were to successfully mate and realize maximal reproductive capacity, the next generation would start with 2,000 potential individuals. If an average of only 100 individuals again survives to adulthood, we then have an approximation of the large reproductive excess needed for colony survival.

Ova of *epixanthe* are typically lycaenine. The outer chorion is highly reticulated and honeycombed in appearance, and frequently covered with

streamers of chorionic secretion. This geometric pattern is uniformly similar to ova of other Nearctic *Lycaena*, particularly congeners of the same subgenus *Epidemia* (Ferris, 1977; Downey and Allyn 1981). Surprisingly among the *Epidemia* there are no appreciable differences in ova size, despite differences in size of adult butterflies. The dimensions of *epixanthe* ova are nearly identical to those published for *dorcas* (Newcomb, 1911), *helloides* (Coolidge, 1924), and *nivalis* (Newcomer, 1911). Differences in size of adults are most certainly accounted for during larval development through the number of genetically-prescribed instars and the condition of the hostplant.

The micropylar region of *epixanthe* ova has a notable configuration that, for all intensive purposes, is indistinguishable from other Nearctic *Lycaena* found in Downey and Allyn's (1981) survey. Some intraspecific variability exists in the number of petal-shaped cells of the micropylar region, but this is common within the *Epidemia* (Ferris, 1977). *Epixanthe* has four to five cells in the rosette, while *dorcas* and *helloides* usually have five to six. The micropyle itself is a small pentagonal depression with five tiny holes at the apices. The same arrangement is shown for *dorcas* by Miller and Brown (1979, Fig. 58) and it is suspected that all *Lycaena* share this pattern. Miller and Brown's (1979, Fig. 57) SEM of *helloides* micropyle is presented by the authors in proof that *helloides* is taxonomically different, but their ovum is so excessively coated with gold/palladium (or possibly vitelline fluid) that the micropyle holes are completely buried and obscured. This is unfortunately interpreted by the authors as a unique taxonomic character.

Beyond the micropylar region, the highly convoluted *epixanthe* chorion encloses a labyrinth of continuous airspace which covers the entire egg surface except for the flat bottom. This constant gas film around the ovum is predicted to serve as a plastron or physical gill allowing gas exchange to occur when the ovum is submerged in water. Bog habitat is often temporarily flooded in late winter and early spring when snows melt and heavy rains set in. At these times, the bog floor may be submerged for several days. Additionally, special structural features of the cranberry leaf guarantee that ova will be covered with water droplets following rains at any time during the year. The cranberry leaf is characterized by its small size, resinous upper surface, and strongly revolute or inrolled lateral margins. Rain water rolls off the hydrophobic upper leaf surface and is easily trapped on the lower surface in the depression between revolute margins. I have seen *epixanthe* ova covered with raindrops retained for two to three days after a routine rainshower. Because of this, plastronic respiration is clearly implicated. To test the hypothesis, further studies are needed to compare the total area of plastronic pores (u^2) with the weight (mg) of the diapausing larva within the egg (Hinton, 1969). In this way only, can plastronic respiration be proven efficient for oxygen

requirements of the larva. Plastronic respiration has been proposed for several lycaenids (Downey and Allyn, 1981), but Hinton's formula-of-proof has not as yet been applied to any lycaenid species. Further studies with *epixanthe* in this regard are pending.

It would be expected that ova that have solved the problem of respiration under wet conditions would also be faced with the problem of water loss under dry conditons. Plastronic pores offer little resistance against dessication and would seem to be detrimental in hot dry weather, especially for small ova with large surface area-to-volume ratios. Some insects have solved the water loss problem by evolving plastron-bearing horns, e.g. *Drosophila*, and maintaining impermeability over the rest of the chorion (Hinton, 1969). In eggs that lack plastron-bearing horns, the same effect may be achieved by having only a small area of the inner chorion permeable to respiratory gases (*loc. cit.*). In *epixanthe* ova, the thick inner chorion (4 microns) is uniformly solid and most likely impermeable except for a small circular area on the dorsum of the egg surrounding the micropylar region. Here the inner chorion is filled with clustered small spongiform air cells that occupy the entire thickness of the inner chorion but do not perforate its surface. If the rest of the solid inner chorion is impermeable as it appears to be, water loss could then be confined to the small spongy area on the dorsum of the egg. In this way, plastronic respiration could function when submerged and water loss could be minimized when dry.

In addition to egg design, *epixanthe*'s microhabitat preference for the cool moist sphagnum carpets on the bog floor undoubtedly also plays a major role in reducing fluid loss. In an experiment outlined above, a balance was indicated between environmental moisture and survival of diapausing larvae: when hostplant leaves were clipped and removed from their microenvironment, they quickly dessicated as did the diapausing larvae within the attached eggs. Such was the problem encountered by Cook and Watson (1908) in the summer of 1907 which precluded their success in rearing *epixanthe* larvae. Thus both egg design and microhabitat contribute to larval survival.

Outer egg chorions of Holarctic *L. phlaeas;* Ethiopian *L. orus* and *clarki;* and Indo-Australian *L. salustius, feredayi,* and *boldenarum* display a rather simple bold cellular pattern with very large chorionic cells and few chorionic ridges (Downey and Allyn, 1981; Clark and Dickson, 1971; Gibbs, 1980). Such a simple chorionic pattern is far less convoluted than ova of Nearctic *Lycaena* and would appear to enclose a significantly smaller intrachorionic airspace. The above species do not diapause as ova and their ovum phase is very brief. It is attractive to speculate that their simple chorionic pattern is related to a different life history strategy and lack of a need for plastronic respiration. By comparison, a large proportion of Nearctic *Lycaena* diapause as ova and have highly-reticulated, finely-cellular chorions. Plastronic respiration would be of decided value for this

group during diapause.

Following diapause, *epixanthe* reaches maturity through a four-instar larval development. Four instars appears to be the typical developmental pattern for most of the Lycaenidae, although an additional fifth instar is reported for some larger lycaenids including some lycaenines. Partial larval descriptions are available for several North American *Lycaena* species, but complete life histories are noticeably few in number. Four instars are reported for *nivalis* (Newcomer, 1911), but five instars for *dorcas* (Newcomb, 1911), *helloides* (Coolidge, 1924), *phlaeas* (Scudder, 1889), and *xanthoides* (Comstock and Dammers, 1935b). New Zealand lycaenines *L. salustius, feredayi,* and *boldenarum* are recorded with four instars (Gibbs, 1980). It would be desirable to compare the larval phases of more *Lycaena* species to determine if a certain prototype adult size (mass) requires a level of vegetative growth that can only be attained through the addition of another larval instar. Caution should be exercised in determining the number of larval instars. Downey and Allyn (1979) have previously pointed out discrepancies in the literature regarding the number of instars of plebejine species. This is a common error and many older studies should be re-examined. The marked differences in trunk size of early and late first instars may be easily confused as two separate larval instars, especially if several larvae are confined together. A reliable index for determining instar numbers is the width of the larval head capsule (Dyar, 1890). The head capsule is heavily sclerotized and relatively fixed in size for each instar. The width is progressively larger in each successive instar and the number of instars is easily determined by the geometrical progression.

The value of complete and accurate life history studies is well demonstrated by Clark and Dickson's (1971) example of two closely-related South African lycaenines which were originally thought to be one species. Primarily on the basis of distributional and larval development differences, a new species *L. clarki* Dickson was discriminated from the older species *L. orus* (Cramer). *Clarki* is slightly larger and matures through a five-instar development, while *orus* is smaller and requires only four instars. In this instance, the fifth instar of *clarki* is an identical morphologic version of the fourth instar except for size. No new setal elements or arrangements appear in the fifth instar. Likewise for Nearctic *Lycaena,* the fifth larval instar seems to be an exact, but larger copy of the fourth instar. Such a conclusion is well demonstrated by use of the specialized mushroom-like secondary seta which serves as a unique marker for maturity of *Lycaena* larvae. This seta occurs in the fourth and last instar of *epixanthe* and *nivalis,* while in *dorcas* and *helloides* the same seta is present in both fourth and fifth instars. In all these examples, the mature larval pattern is already present by the fourth instar. Such data suggest that the four-instar development is the basic lycaenid pattern and evolutionary changes toward larger adult size are accomodated by adding another identical

instar.

Epixanthe larvae in all phases are well-designed for concealment within the cranberry bog environment. An ontogenetic progression of programmed defenses help protect the larvae during development. Young larvae are present in the spring before new cranberry shoots appear and feed totally concealed on the undersurfaces of older evergreen leaves. They are boldly marked with red dorsal stripes which effectively camouflage them on the anthocyanin-tinged vegetation of early spring. This protective red-on-green pattern of early instars is found frequently among lycaenid larvae and correlates well with colors of the hostplant during early larval development. Other red-on-green lycaenid examples that immediately come to mind are *L. nivalis* (Newcomer, 1911), *Plebejus (Agraides) aquilo* (Day and Jackson, 1980), and *Callophrys (Incisalia) augustinus* and *polios* (Ziegler, 1953). Later instars are generally present about the time new cranberry shoots unfurl and begin to grow rapidly. Anthocyanin pigments disappear from the cranberry about this time and the late larvae feed in exposed positions on the new green shoots. These instars, for the most part, have green non-striped bodies.

In accordance with exposed feeding, the body surface of later instars has a subdued matt appearance which provides considerably less spectral reflectance than the semi-gloss surface of earlier instars. The morphological basis of this phenomenon is found in the ultrastructure of the larval integument. The first instar integument is relatively flat and smooth, interrupted only by small widely-spaced microtubercles. Spectral reflectance of this instar is high, since a large proportion of the integument is oriented in one plane. Following the first instar, a radical change in the microanatomy of the integument takes place. The fundamental pattern switches to a geometrical arrangement of large oval depressions in the epicuticle. This type of sculpturing is known as the "macro"-type (Byers and Hinks, 1973). Each "macro" surface unit is the product of a single underlying hypodermal cell. When surface units are smooth and oriented to provide a large reflecting area, as they are in the second instar, the epicuticle appears shiny or semi-glossy. Thus both the first and second instars have a relatively bright body surface, although they are ultrastructurally different. Their behavioral concealment on leaf undersurfaces and camouflaged markings reduce the value of adaptive modifications to the larval integument of early instars. On the other hand, a matt appearance with reduced reflection would appear to have an adaptive value in making the exposed older larvae less conspicuous. Reduction of spectral reflectance in later instars is accomplished by the addition of thin vertical partitions around each epicuticular "macro" unit giving the integument a honeycombed appearance. These partitions, absent in the second instar, are extremely effective in light scattering and diffusion. Byers and Hinks (1973, Fig. 12), in their ultrastructural survey of the

lepidopterous larval integument depict an example of the integument of *L.hyllus (=thoe).* The similarities to *epixanthe* are immediately obvious. After studying several additional scanning micrographs kindly loaned by J. R. Byers (pers. com.), it is concluded that the larval integument of *hyllus* and *epixanthe* are ultrastructurally identical. It is suspected that this type of integument may be universal within *Lycaena.* Recent integument SEM's from New Zealand (Gibbs, 1980) of larval *L. feredayi* and *boldenarum* show identical integument morphology with *hyllus* and *epixanthe.* This tends to strengthen the argument for universality.

A great deal of emphasis in this study is placed on the ultrastructure and chaetotaxy of the first instar *epixanthe* larva. There is no thorough treatment of any *Lycaena* species on this subject in the literature. The importance of the first instar larva comes from the widespread belief among larval morphologists that this instar is a specialized embryonic stage reflecting primitive characters of an archetype larva. Consequently, by comparing the arrangement of first instar larval characters of many species within a given taxon, patterns of relatedness and divergence may be implied. The paucity of chaetotaxy studies within Lycaenidae is due in large part to the minute size of lycaenid larvae and the limits of resolution by light microscopy. Setal mapping is greatly facilitated by use of the scanning electron microscope and this instrument should become the standard for detailed studies of first instar lycaenids.

The overall configuration of the *epixanthe* first instar cranium differs only in minor detail from the few other lycaenids studied. Lateral adfrontal sutures extend dorsally to the cervical musculature without meeting in the midline, thereby leaving the frons open. While this condition is uncommon in lycaenids, it is not unknown. Scudder (1889, Pl. 79, Figs. 27 &42) found the head capsule of *Callophrys (Mitoura) gryneus* and *C. (Incisalia) irus* with an open frons. Curiously, he missed the open frons of the solitary *epixanthe* larva he dissected. Appendages of the *epixanthe* cranium are very much like those of *Everes comyntas* and *Leptotes cassius theonus* (Lawrence and Downey, 1966; Downey and Allyn, 1979). The *epixanthe* mandible has five teeth instead of the six to seven teeth found on the plebejine mandible and the *epixanthe* labral puncture sits centrally in the labral notch instead of between setae M1 and M3. Some minor differences also exist in the number of setae on the basistipes, but the most interesting difference is found in the sculpturing of the hypopharynx. The *epixanthe* hypopharynx consists of a smooth spineless lingula and a midline trough along the floor of the mouth. The latter is flanked on both sides by fleshy lobes of the paraglossae which bear tiny microspines paired in twos. The plebejine hypopharynx, on the other hand, is spiny over its entire surface and spines are not limited to the paraglossae. As suggested by this small comparison, the arrangement of hypopharyngeal spines could eventually prove to be of taxonomic value. This concept was first promoted by

Downey and Allyn (1979) and awaits further comparative studies.

Chaetotaxy of the *epixanthe* cranium is quite simplified. It too resembles the aforementioned plebejines with minor modifications. Hinton (1946) states that a broad uniformity of lepidopteran cranial setae is found throughout the order and a general primitive pattern is preserved. He feels that few modifications of the primitive pattern have occurred during adaptive radiation, plus adjustments that have taken place generally did so through slight changes in position and relative lengths rather than through acquisition of new setae. Because of general uniformity throughout the order, cranial chaetotaxy is of little value in separating families. However, slight minor differences become important in determining genera and species. Cranial setae of *epixanthe* fall roughly into two groups: 1) long tactile setae clustered anteriorly on the head capsule which project forward ready to contact objects in front of the larva, 2) short proprioceptors scattered posteriorly which provide information regarding head position when deeply retracted into the prothorax. Each setal group on the retractable portion of the head is significantly reduced in length and number. All setae of this area are microscopic in size and setae A3, O2, O3, L1, P2, and V3 are absent. This condition represents a somewhat greater modification than that found on the retractable head capsule of *E. comyntas* and *L. cassius*.

Setal arrangement on the thorax and abdomen shows more variability throughout the order than cranial setae and, as such, becomes a useful tool for distinguishing species, genera, and even families (Hinton, 1946). Before discussing chaetotaxy of the *epixanthe* larval body, a short introduction seems in order. Three classes of setae (primary, subprimary, secondary) are recognized on the lepidopterous larval body. Primary setae are those that are present on the first instar and remain essentially unchanged through subsequent instars. These setae are the dominant features of the first instar and are thought to represent primitive setae derived from an archetype larva (*loc. cit.*). In this line of thought, closely-related species are expected to show some degree of setal homogeneity and unrelated species to show divergent setal patterns. Secondary setae are not present on the first instar, but make their appearance on the second and later instars. In evolutionary terms, these setae are thought to be more recently acquired in the history of the organism and represent responses to varying environments. In certain families like Lycaenidae, they tend to be very numerous and sometimes highly modified in appearance. On certain occasions, modified secondary setae can become so distinctive as to effectively serve as a marker for a given group (e. g. "mushroom" seta of late *Lycaena* larvae). Subprimary setae are more common in primitive families and by definition are not present on the first instar, but appear in subsequent instars as new setae situated in constant positions very much like primary setae. They are always few in number. There is a tendency for

certain setae (L3) which are subprimary in primitive families to appear regularly in the first instar of more highly specialized families (e.g. Lycaenidae). As such, they should be treated as primary setae and mapped accordingly.

On the first instar *epixanthe* larva, five different types of primary setae occur. Long spiculiferous tactile setae and tiny proprioceptive microsetae are by far the most common. Their large numbers attest to the important sensory roles they perform. They are arranged in recognizable patterns on the body surface and are convenient characters for comparative mapping. Lenticles likewise are a prominent feature of the first instar integument. They are given various names by other workers (annuli, cornicula, crateriform papillae, hairless tubercles, perforated cupolas) and appear to serve a glandular or sensory function. While they are not derived from setae, they do have an orderly arrangement on the first instar and can be mapped along with primary setae.

In contrast to the cranium, the setal map of *epixanthe* thorax and abdomen is considerably different from that of the published Plebejinae (Lawrence and Downey, 1966; Downey and Allyn, 1979). Unfortunately, no setal maps of other *Lycaena* species are available for comparison. Very few descriptions of first instar *Lycaena* exist in the literature, e.g. *phlaeas* (Scudder, 1889), *hyllus (loc. cit.), nivalis* (Newcomer, 1911), *dorcas* (Newcomb, 1911), *helloides* (Coolidge, 1924), *xanthoides* (Comstock and Dammers, 1935b), *orus* (Clark and Dickson, 1971), *clarki (loc. cit.)*, and *feredayi* (Gibbs, 1980). All are brief and poor in setal descriptions. The only broad generalization that can be drawn is the uniform presence of prominent double rows of dorsal setae, D1 and D2, and a skirt of prominent lateral setae. These setal groups are not unique to *Lycaena*, but common throughout the Lycaenidae. Most interestingly, the row of D2 setae terminates at the sixth abdominal segment in *epixanthe, dorcas, nivalis, phlaeas, orus*, and *feredayi*. These butterflies represent a distributional spectrum from Nearctic, Holarctic, Ethiopian, and Indo-Australian realms. The precise uniformity of their dorsal setae suggests that primary dorsal setae have changed little from proto-*Lycaena*. The only species with which more than a superficial comparison could be made with *epixanthe* is the South African *L. orus* and the New Zealand *L. feredayi*. Clark and Dickson (1971, Pl. 47) depict the entire life history of *orus* in a detailed hand-colored composite. Gibbs (1980, Pl. 163) includes an exquisite color photograph of *feredayi* first instar. Setal descriptions are absent in both texts, yet the graphic resemblance to *epixanthe* stands out immediately. Major setal groups, anal shields, and subdorsal and supraspiracular lenticles appear nearly identical to those of *epixanthe*. Details of the cranium, prothoracic shield, and venter are lacking, but the degree of homogeneity thus far determined is noteworthy. During geologic history, the North American continental plate and the conjoined Antarctic-

Australian plates (with New Zealand still attached) are believed to have completed separation from the African plate in the late Cretaceous approximately 100 million years ago. In view of this, the resemblance of *orus, feredayi,* and *epixanthe* first instars attests to the profound tendency to preserve archetype characters in first instar larvae of the genus.

The *epixanthe* prothoracic shield is a distinctive anatomic structure which awaits comparison with other *Lycaena* species and may be taxonomically useful. The *epixanthe* shield supports four sets of primary setae and a pair of lenticles in the first instar. Most of the setae are tactile in type, but a unique filiform seta, XD2, differs from the others. It originates from a depressed puncture-like opening in the rear of the shield and vibrates strongly in air currents. Hinton (1946) in his study of moth larvae routinely found a puncture, XDa, near the base of XD2 and often used this puncture to establish the certainty of XD2 identification. It is easy to speculate this puncture may have been incorporated into the base of XD2 in higher specialized families like Lycaenidae. XD2 is the only shield seta that can be traced completely through *epixanthe* larval ontogeny. In later instars, intense secondary setosity covers the entire larva and XD2 becomes the only clearly-identifiable primary seta remaining on the body. Lawrence and Downey (1966) were able to trace two shield setae, XD2 and SD1, through *E. comyntas* larval ontogeny. Following *epixanthe*'s first molt, a radical change takes place in configuration of the shield, analogous to the change observed in integument sculpturing. A new transformed shield makes its appearance in the second instar and from there on fundamentally remains the same in subsequent instars. It is quite clear that many characters of the first stage of larval life (e.g. integument, shield, setation, spiracles, proleg crochets) are distinctly differentiated from remaining larval stages.

Setation of the anterior and posterior extremes of the lycaenid larval body are unique areas that may also prove to be taxonomically useful. In *epixanthe*, the anterior margin of the first instar prothorax contains a row of long tactile setae that together with shield setae project forwardly over the larval head. This condition is common within lycaenids where the dorsal region of the retractable head lacks its own tactile setae. Using Hinton convention, Downey and Allyn (1979) designated the prothoracic setae as MD1, MSD1, MSD2, and L1. Although the first three setae bear a nomenclatorial "M", they are not microsetae in the true sense. In *epixanthe*, these setae are all long and tactile. Nevertheless, a microsetal origin cannot be ruled out. Ultrastructural studies of first instar *Brephidium pseudofea* (Morrison) show that MD1 in this species is small and microseta-like (Wright, unpubd. data) which is the first evidence these setae may have a microsetal derivation. Hinton (1946) states that MD1 is not present on the thorax, yet he emphasized that various setae on the body of higher specialized families may undergo elongation, multiplica-

tion, fusion, and other assorted modifications. Whatever their origin, it is clear that MD1 and the MSD group evolved on the lycaenid prothorax to form a protective fringe of tactile setae over the head and neck.

At the posterior end of the larval body, *epixanthe*'s ninth and tenth abdominal segments are distinctly separate and marked by a clearly visible intersegmental cleft. This is in contrast to the terminal portion of the plebejines *Everes comyntas* and *Leptotes cassius* where A-9 and A-10 appear fused as one segment (Lawrence and Downey, 1966; Downey and Allyn, 1979). *Epixanthe*'s narrow ninth segment is reduced in setation as well as size. MD1, D1, SV1, and MV3 are present on the contracted segment and only one lateral seta occurs. Hinton (1946) correctly recognized that Rhopalocera usually have only one lateral seta on the ninth segment (L1). *Epixanthe*'s tenth segment has three major lateral setae on the body fold (L1-3) which reside in a continuous line with lateral setae of previous abdominal segments. On a line slightly ventral to these setae, directed posteriorly, are two tufted setae whose terminal ends dangle over the anal opening. These setae are easily differentiated from lateral setae by size and appearance. Downey and Allyn (1979) in their study of *L. cassius* incorporated these tufted setae into the lateral setal group of fused A9-10. In doing so, they derived a total count of six lateral setae (three for A-9 and three for A-10). Some of their A-9 setae are clearly in the province of A-10 and I have reason to believe this setal arrangement is incorrect. It seems quite improbable that a full complement of A-9 lateral setae (L1-3) exists on the fused A9-10 plebejine segment. An equally-balanced fusion of two complete anatomical units would be a rarity. A much more logical event during the course of evolution would be an initial attenuation or reduction of one or another segment, followed by its fusion with a neighbor segment or complete disappearance. Since many lepidopteran families, and especially lycaenines, have a small A-9 segment with reduced setation, the course of plebejine evolution could not have been much different. It would seem logical that the plebejine A-9 fused with A-10 only after it was initially diminished in size. In this analysis, the lycaenid A-9 may be regarded as an evolutionary "degenerate" unit and A-10 as a very highly-specialized unit. I would recommend that any system of setal names used to describe the terminal segment(s) of lycaenines and plebejines employ only one A-9 lateral seta.

The *epixanthe* tenth abdominal segment also has a dorsal (anal) shield and a row of unique subanal setae. The shield is very weakly sclerotized and recognized only by its slightly depressed nature. No setae originate from the shield, but two lenticles appear on each lateral margin. *Epixanthe*'s shield is identical to that pictured for the South African *L. orus* (Clark and Dickson, 1971) and *L. feredayi* from New Zealand (Gibbs, 1980). All in all, judging from its sparse decoration, the lycaenine anal shield will probably prove to be of little taxonomic value in comparative

studies. A more interesting region of the tenth segment is the subanal fold where a row of small setae sweeps beneath the anal opening. Six setae are found on each half of the segment, beginning on the lateral aspect of the anal proleg and coursing to the midline beneath the anal slit. The entire row is derived from anal proleg setae. It was originally thought that two of the setae on the lateral aspect of the proleg represented subventral setae SV1 and SV2, but it is now believed that SV1 and SV2 don't occur on A-10. The two setae in question are situated considerably below the subventral line and aligned with ventral proleg microsetae of previous segments. Furthermore, one seta is thorny in configuration unlike any seta of the SV group. Other thorny setae are found in the subanal row which clearly attests to the relatedness of the entire subanal series.

The architecture of the terminal portion of the tenth segment appears to be designed to facilitate expulsion of frass (Downey, pers. com.). It is not uncommon when observing live larvae to see expelled frass pellets momentarily "hang-up" behind the anus and then drop free several seconds later. The row of subanal setae may serve as a ledge to catch frass pellets and prevent them from lodging beneath the body. Similarly, the tufted setae on the suranal fold may prevent frass from tumbling over the top of the body when the larva is inclined head-down. In this way, frass pellets may be safely guided away from the body. Newcomb (1911) in his description of first instar *dorcas* larvae referred to "two small branched spines project(ing) caudad from the last segment, just below the anal opening." These "branched spines" may very well be identical to the thorny setae found in the subanal row of *epixanthe*. This region is fascinating and future comparative studies of lycaenid larvae should include its examination.

The value of certain inconspicuous minor larval characters remains unknown, but the effort to examine them may be worthwhile. Some regional areas with promise are the spiracles and ventral prolegs. The internal sculpturing of larval spiracles is very elaborate and detailed. Sieve-like patterns within the spiracular lumina are presumed to prevent dust, foreign bodies, parasites, and even water from entering the tracheal system. At this time, very little information is available regarding spiracle microanatomy of lycaenid larvae. They are readily accessible to study by SEM and their changing geometrical designs during ontogeny seem to offer a fertile field for investigation. Lastly, the ventral prolegs are frequently overlooked in descriptive works, but they too are easily studied with SEM. Each first instar *epixanthe* ventral proleg has a uniordinal mesoseries of eight crochets divided into two equal groups by a median fleshy lobe. An interrupted mesoseries of this type is diagnostic of the Lycaenidae, but it is now known that the number and size of first instar crochets may vary between species. For example, eight crochets occur on the *epixanthe* proleg, but only four are found on the prolegs of the

plebejines *E. comyntas* and *L. cassius*. (See also discussion of later instar prolegs below.)

In concluding the discussion of the *epixanthe* first instar, it is important to point out again that the first stage of larval life is morphologically differentiated from the remaining stages. Changes in some larval characters at the first molt are so profound that it is sometimes difficult to imagine the initial two instars represent the same species. However, after the first molt, most larval characters remain fundamentally unchanged and subsequent molts thereafter yield only minor modifications. This pronounced transformation of the primitive first instar to the second instar is viewed as a major step in ontogenetic progression. Changes that occur at this point were described by Scudder (1889) as "hypermetamorphosis". In the true sense of the word, larval metamorphosis is represented by all larval stages taken together. Yet within the general framework of larval metamorphosis, "hypermetamorphosis" may be looked upon as a specialized form of change that transforms the primitive archetype larva into the "advanced" later larva which enjoys all the adaptive characters gained through evolution.

After the first instar, patterns of setosity on the larval body tend toward greater and greater numbers of secondary setae. Eventually, the later instars become so densely covered with secondary setae that the original primary setal pattern is totally obscured and perhaps even non-existent. Seta XD2 on the prothoracic shield is the only seta of later instars that can be positively identified as a primary seta.

Near the end of larval ontogeny at the beginning of the fourth instar, a new specialized form of modified secondary seta makes its appearance for the first time. This seta resembles a tiny white mushroom and is considerably smaller than the major spiculiferous setae. It is scattered over the larval integument in typical secondary setal fashion, reaching numbers of 55-65 per segment. Its ultrastructure was unknown until it was included as an incidental finding on the cuticle of *L. hyllus (=thoe)* in Byers and Hinks' (1973) SEM survey of lepidopterous larval integument. This seta is identical in both *epixanthe* and *hyllus* and it is now known to occur throughout the genus *Lycaena*. It is variously described in older literature as white granulations, wartlets, vibrissae, ovoid tubercles, bulbous processes, egg-shaped processes, globe-like setae, pom-pom setae, and mushroom-shaped appendages. To date, the unique seta has not been found in any other lycaenid genera and it is virtually certain that it is an effective marker for mature *Lycaena* larvae. The following *Lycaena* species have been recorded with the seta: *arota* (Comstock, 1928), *xanthoides* (Comstock and Dammers, 1935b), *editha* (Scott, 1979), *hyllus* (Scudder, 1893), *heteronea* (Williams, 1910), *dorcas* (Newcomb, 1911), *helloides* (Coolidge, 1924; Comstock, 1929), *nivalis* (Newcomer, 1911), *hermes* (Comstock and Dammers, 1935a), *dispar* (Whalley, 1979), *orus*

(Clark and Dickson, 1971), *clarki (loc. cit.), feredayi* (Gibbs, 1980), *salustius* (*loc. cit.*), and *rauparaha (loc. cit.)*. No mention of this seta could be found in the vast literature for the widely-distributed *phlaeas*, which is a common butterfly that has been reared countless times without record of the unique seta. I was kindly loaned a *phlaeas* pupal specimen from the New York State Museum, Albany, NY, collected over one hundred years ago by past State Entomologist Jos. Lintner. The last instar exuvia was recovered from the loosely-constructed hibernaria surrounding the pupa. Under SEM examination, the larval setae were still clearly intact and visible on the century-old exuvia. It can now be positively stated that mature *phlaeas* larvae possess the specialized mushroom-shaped secondary seta.

Mature *epixanthe* larvae have a broad arrow-shaped prothoracic shield, quite differentiated from the first instar shield. This configuration is apparently uniform within the *Lycaena*, as it is shared by mature larvae of *arota* (Dyar, 1891), *xanthoides* (Comstock and Dammers, 1935b), *nivalis* (Newcomer, 1911), *hermes* (Comstock and Dammers, 1935a), *orus* (Clark and Dickson, 1971), *clarki (loc. cit.), salustius* (Gibbs, 1980), *rauparaha (loc. cit.), feredayi (loc. cit.)*, and *boldenarum (loc. cit.)*. Setation of the large mature shield is considerably reduced and XD2 is the only primary seta found in *epixanthe*. This seta is also commonly present on the mature shield of plebejines. Curiously, in New Zealand *Lycaena*, XD2 is present on the mature shield of *feredayi*, but absent on *boldenarum* (Gibbs, 1980, SEM Figs. 51 & 54). The latter species also lacks the characteristic mushroom-shaped secondary seta found on the integument of many other mature *Lycaena* larvae. (See above.) Previous studies of adult *boldenarum* have shown that this unique butterfly may warrant distinct generic status (Sibatani, 1974). Further SEM examination of *boldenarum* and comparative studies of other lycaenine immatures may facilitate taxonomic decisions in this regard.

The pattern of proleg crochets, like other integument derivatives, also changes in later instars. Each proleg of the mature *epixanthe* larva has a large mesoseries of 60-70 crochets. These crochets are organized into two separate multiseries separated centrally (as in the first instar) by a fleshy spatulate lobe. Most significantly, a new element makes its appearance on the lateral aspect of the mature larval proleg. This element consists of a small horizontal row of five equal-sized crochets (uniordinal lateroseries) which are consistent in number from leg to leg. This lateroseries is found on other Nearctic (*hyllus, arota*) and Palearctic (*virgaurae, tityrus, helle*) species, but it proves not to be a unique lycaenine character as it is present in riodinids as well (Downey, pers. com.). However, this does not detract from its usefulness for comparative lycaenine studies. Gibbs (1980, SEM Fig. 45) has shown in New Zealand *Lycaena* that considerable interspecific variability exists in the number of crochets of the lateroseries.

Pupae of *epixanthe* are very small and obtect. They resemble the general lycaenid pupa in shape and display the same type of fine surface reticulations. Most of the pupae are green in color and heavily marked with black maculations making them quite inconspicuous when hidden among the cranberry leaves and sphagnum moss. Not all pupae are green and an unusual polymorphism exists for pupal color. Approximately five percent of the pupae are purple. Despite their atypical color, these pupae also blend imperceptibly into the speckled shadows of the cranberry vines and sphagnum on the bog floor. Origins of pupal polymorphism are not known, but they may occur widely in the lycaenine stock. Newcomb (1911) in his studies of *dorcas* reported small numbers of black puape and in a single instance a pupa colored "purple-madder".

The *epixanthe* pupal integument contains several unique cuticular derivatives (spiracle sculpturing, stridulatory organ, setae). Like those of the larva, lumina of pupal spiracles are decorated with coral-like sculpturing. This sculpturing is morphologically differentiated from larval spiracles, but a similar protective role is hypothesized for both. Virtually nothing is known about lycaenid pupal spiracles. A detailed study seems in order to determine if interspecific variability exists and if it can use taxonomically.

Like other lycaenids, *epixanthe* pupae contain a well-developed stridulatory organ located on the dorsum of intersegmental region A-5/A-6. The sound organ consists of a stridulatory file on A-6 with recurving teeth that grate against surface irregularities (grains and reticulations) of the stridulatory plate on A-5. This configuration is identical to the typical *Lycaena* sound organ found by Downey in eleven species of Palearctic and Nearctic *Lycaena* (Downey, 1966; Downey and Allyn, 1973).

The trumpet-shaped seta of *epixanthe* pupae is shared by many other *Lycaena* species. This seta was first described from the pupal case of *phlaeas* by T. A. Chapman (1905a) as a "trumpet-hair". Chapman subsequently recorded the same seta in other Palearctic *Lycaena* and speculated on its universal occurrence within the genus (Chapman, 1905b, 1906, 1907, 1913). The seta has since been recorded in *L. orus* and *clarki* (Clark and Dickson, 1971) of the Ethiopian realm; *L. salustius, rauparaha,* and *feredayi* (Gibbs, 1980) of the Indo-Australian realm; plus in Nearctic members *arota* (Comstock, 1928), *xanthoides* (Comstock and Dammers, 1935b), *editha* (Scott, 1979), *gorgon* (Comstock and Dammers, 1934), *hyllus* (Scudder, 1889), *heteronea* (Williams, 1910), *dorcas* (Newcomb, 1911), *helloides* (Coolidge, 1924; Comstock, 1929), *nivalis* (Newcomer, 1911), and *hermes* (Comstock and Dammers, 1935a). The seta has not been found on pupae of other lycaenid genera. Its ultrastructure was recently depicted by Downey and Allyn (1973, Figs. 60 & 61) and Gibbs (1980, Fig. 49). Downey and Allyn (1973) also noticed very small numbers of a second setal type (hydroid-type) on the sixth abdominal segment of some *Lycaena* species, but not others. This hydroid seta was present on

dispar and *hyllus* pupae, but absent on *phlaeas* and *helloides*. The author did not find it on *epixanthe* pupae.

In conclusion, the author has attempted to elucidate *epixanthe*'s unique life history strategy for survival in the bog, while underlining the striking homogeneity of morphologic and development characters within the genus. Reproductive biology of adult butterflies is tightly coordinated with the hostplant flowering period, but success of the species is most likely linked to adaptive features of its ova and larval stages. The great majority of the butterfly's lifespan (85%) is spent in the egg stage where plastronic respiration is hypothesized to occur in order to circumvent the frequent hazard of submergence in flood water and rain water. Ova architecture consistent with plastron breathing is found within the highly sculptured topography of *epixanthe*'s chorionic coats. Many other overwintering Nearctic ova have comparable external sculpturing, suggesting that evolution of the *Lycaena* plastron may have been accomplished very early in the Nearctic line. Following the egg stage, larval ontogeny commences with first instars which are fixed with primitive features thought to reflect those of the lycaenine archetype. Comparative studies of *Lycaena* first instars are quite preliminary at this time, but early evidence points toward considerable homogeneity. It may be that morphologic conservatism has resulted in very little change in first instars during the course of evolution. After the first larval molt, a radical change takes place in larval anatomy and subsequent instars take on a substantially different appearance (hypermetamorphosis). As larval stages progress, integument derivatives of late *Lycaena* larvae still show striking comparative homogeneity, but patterns of larval coloration and behavior notably diverge in response to contrasting habitats and food preferences. It is through these latter adaptive modifications that *Lycaena* larvae will probably be found to differ most significantly. The same principle is also expressed in lycaenine pupae. The author cautions that many further ultrastructure studies of lycaenine immatures are needed to determine if certain characters show greater variability between congeners than others. Only then can the reliability and usefulness of immature characters be evaluated for taxonomic decisions.

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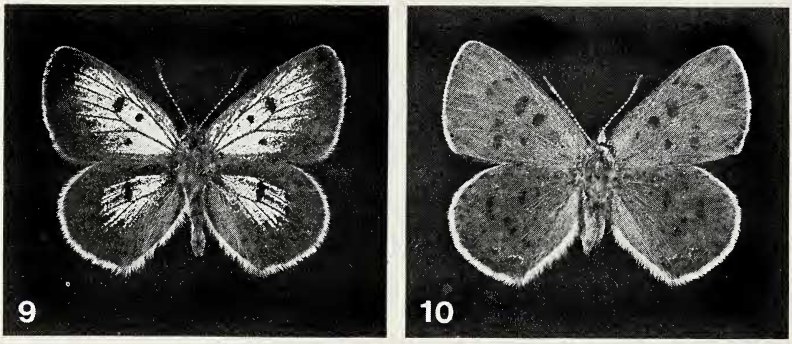


Figs. 9-10. Ultraviolet photography of adults. Forge Pond bog, Atlantic Co., N.J. **9.** Male. **10.** Female.

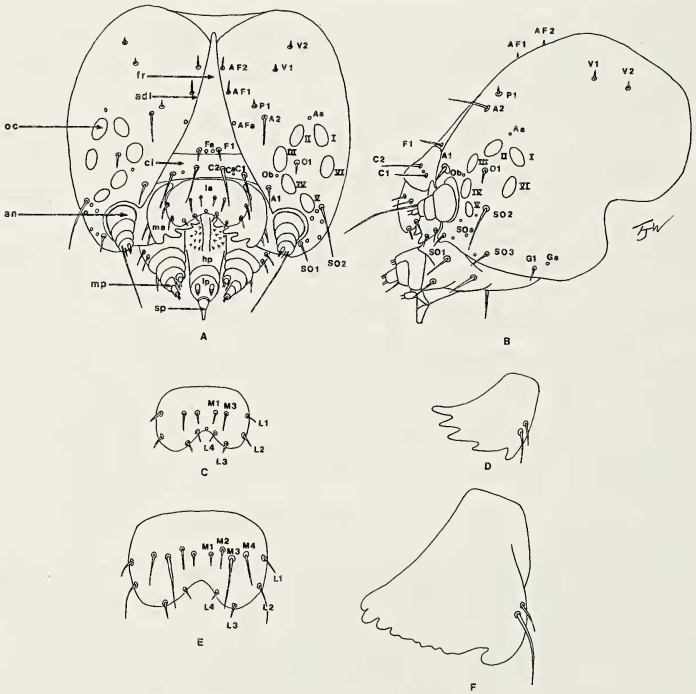


Fig. 11. Cranial chaetotaxy, first instar. A. Frontal view. B. Lateral view. C. Labrum, first instar. D. Mandible, first instar. E. Labrum, fourth instar. E. Mandible, fourth instar. Key to abbreviations: adl=adfrontal lateral suture, an=antenna, cl=clypeus, fr=frons, hp=hypopharynx, la=labrum, lp=labial palps, ma=mandible, mp=maxillary palp, oc=ocellus, sp=spinneret. Setal names and punctures explained in text.

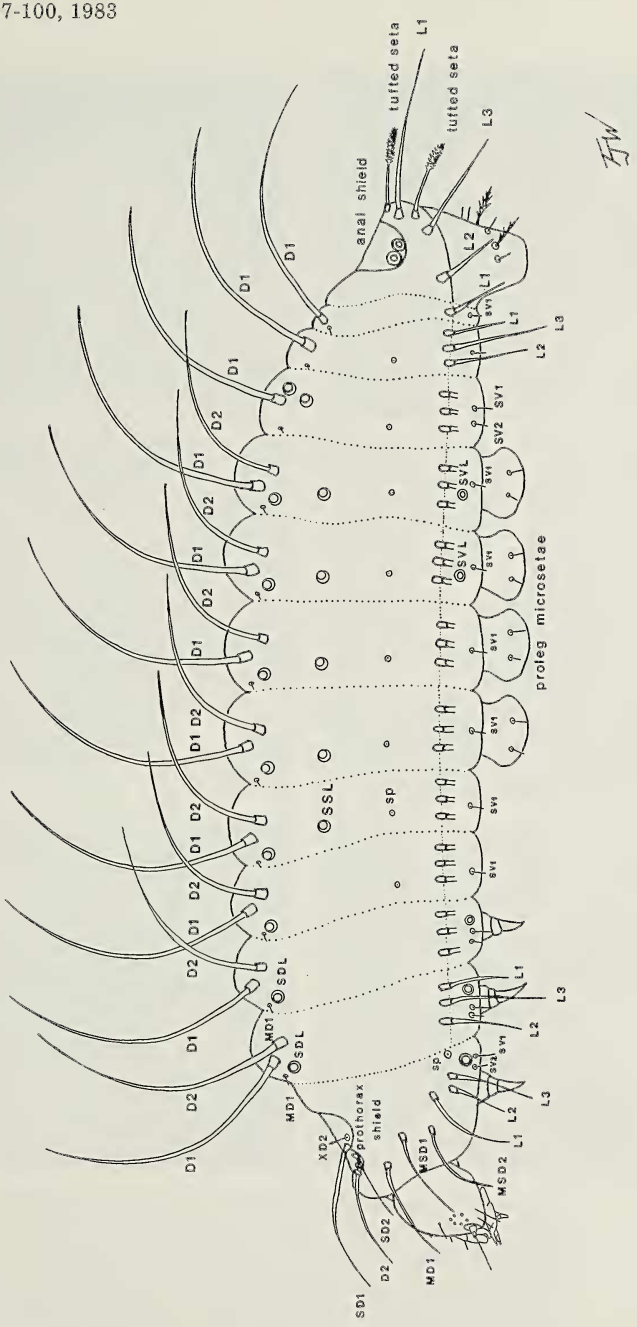


Fig. 12. Chaetotaxy of body, first instar. Left side labeled only.

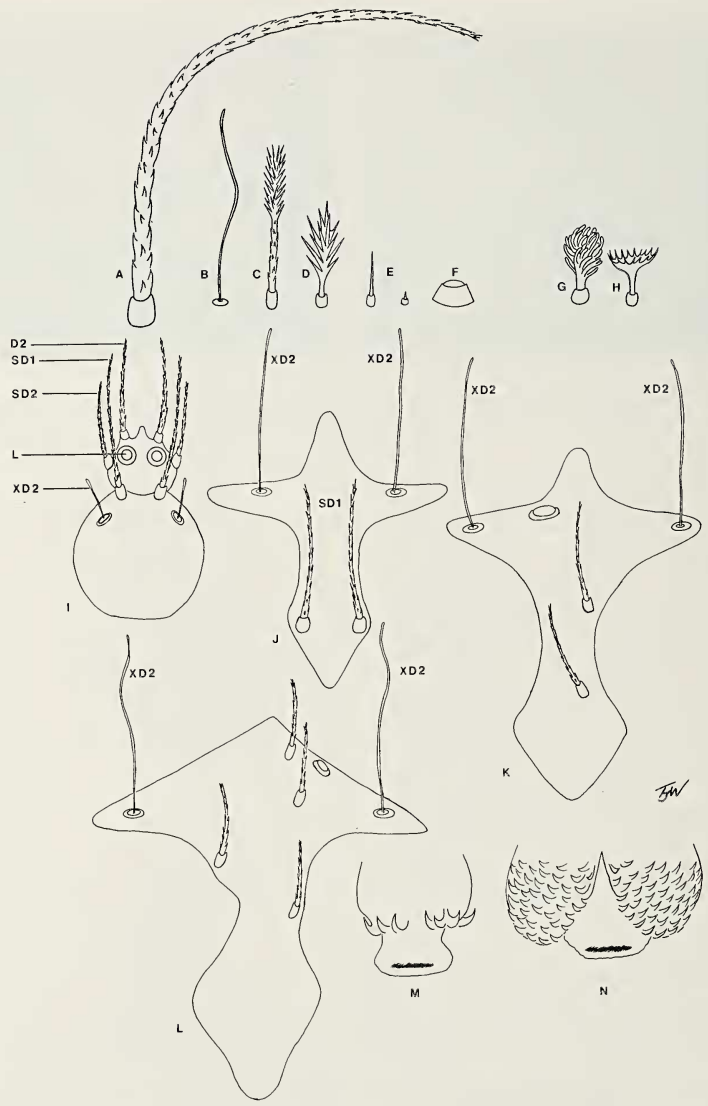
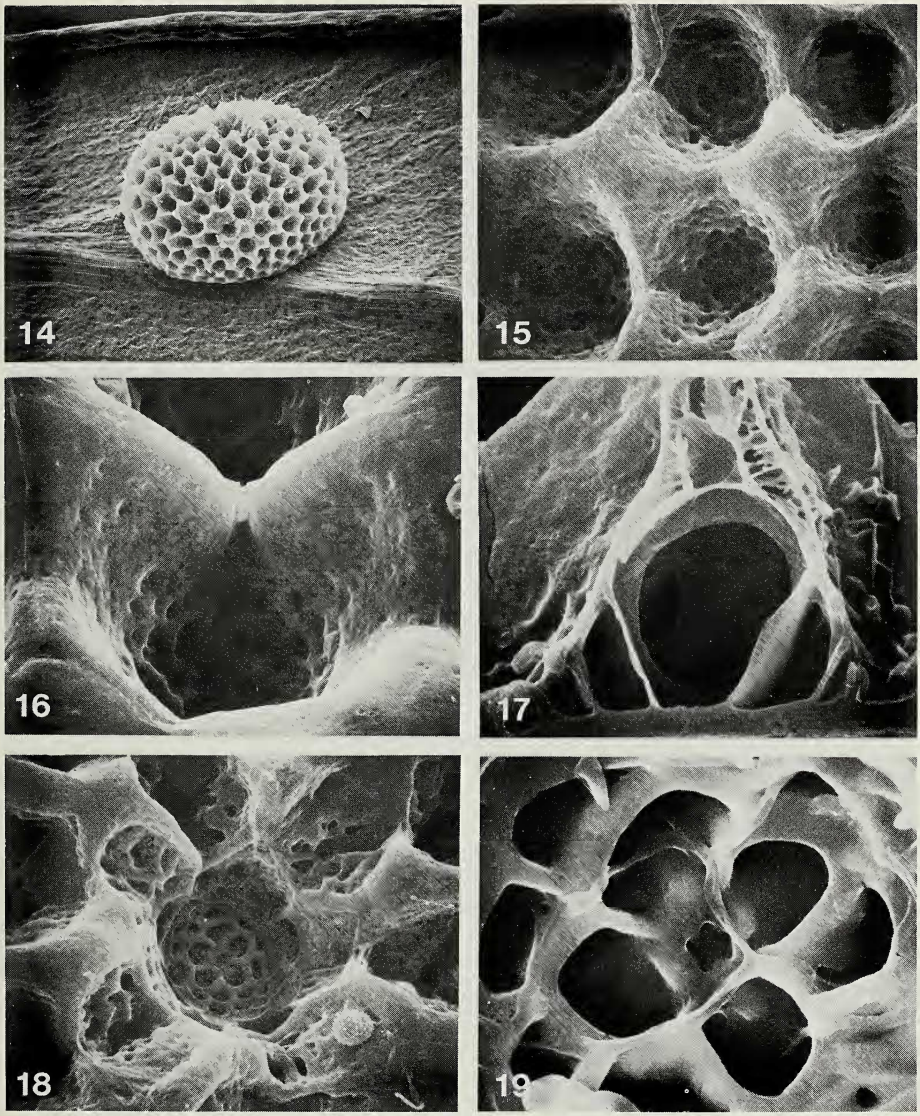
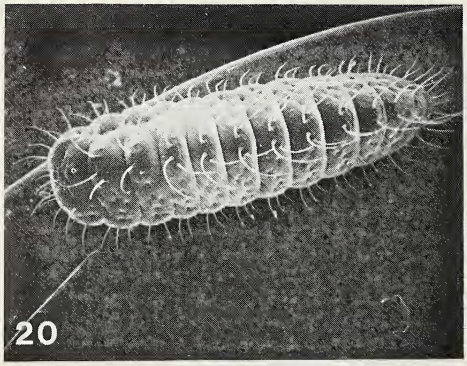
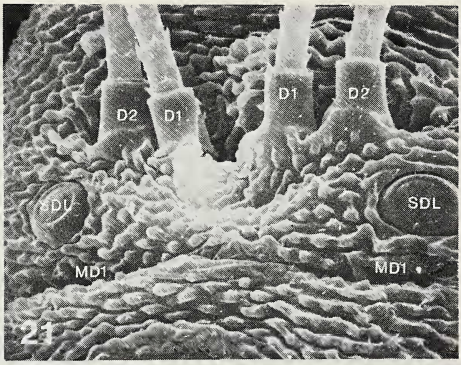


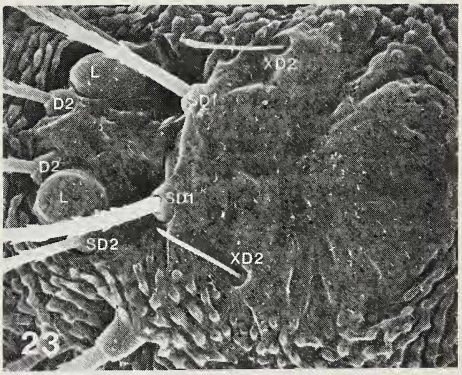
Fig. 13. A-E. Types of setae, first instar. A. Major spiculiferous seta. B. Filiform seta. C. Tufted seta. D. Thorny seta. E. Smooth non-spiculated setae, long tactile and short proprioceptive. F. Lenticle. G. Specialized secondary seta, fourth instar. H. Trumpet-hair seta, pupa. I-L. Prothoracic shield of first (I), second (J), third (K), and fourth (L) instar. M-N. Ventral prolegs, medial surface of first (M) and fourth (N) instar.

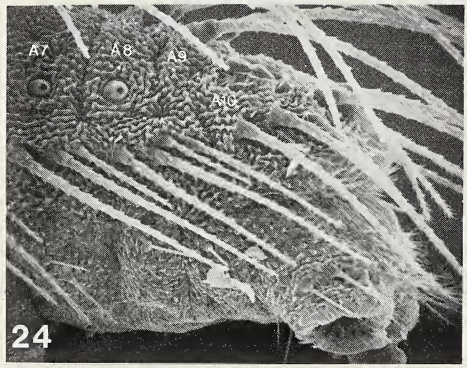


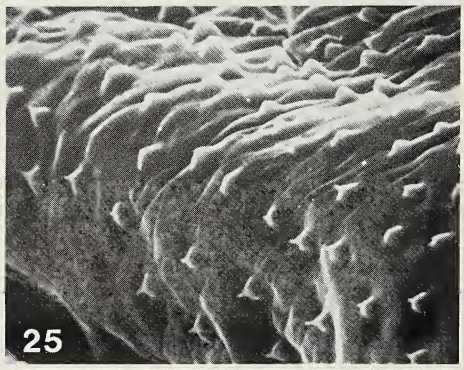
Figs. 14-19. SEM of ova. 14. Dome-shaped ovum with honeycombed chorion on undersurface of cranberry leaf. 80x. 15. Chorionic reticulum showing ridges and cells. 640x. 16. Chorionic cell. Note aeropyles at bottom of cell and thin membrane between ridges. 1250x. 17. Fractured chorion showing intrachorionic airspaces. 2100x. 18. Micropylar region. Pollen grain at lower right. 640x. 19. Micropyle and micropylar rosette. 2500x.



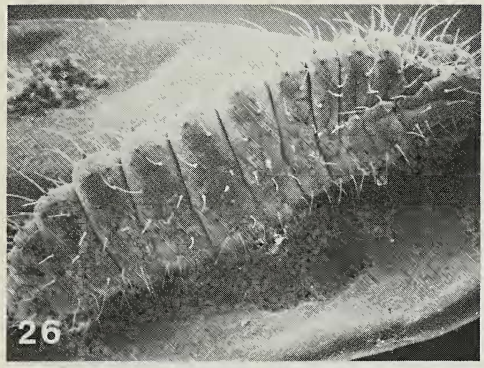


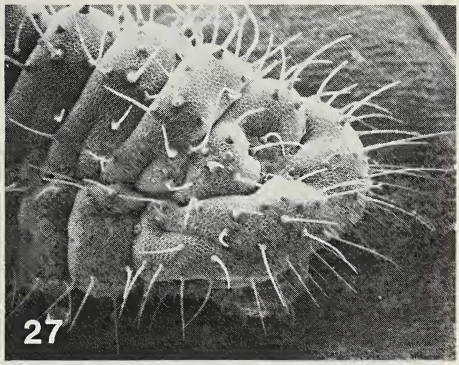


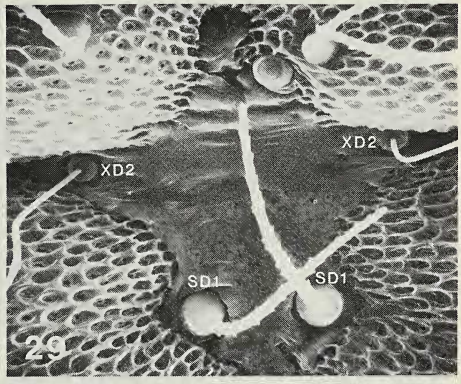


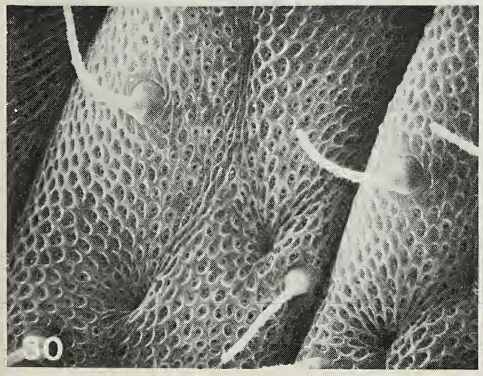


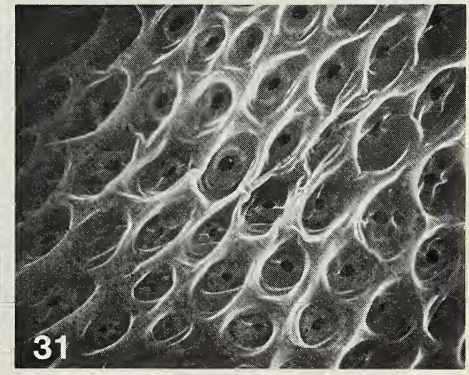
Figs. 20-25. SEM of first instar. 20. Whole larva, dorsal view. Anterior segments on left. Note setation and integument pits. 40x. 21. Mesothorax, dorsal view. Anterior margin of segment at bottom. 700x. 22. Larval head retracted into prothorax, frontal view. 410x. 23. Prothoracic shield. Anterior portion of shield at left. 640x. 24. Terminal segments of abdomen, lateral view. 320x. 25. Integument sculpturing. Note flat surface with microtubercles. 2180x.



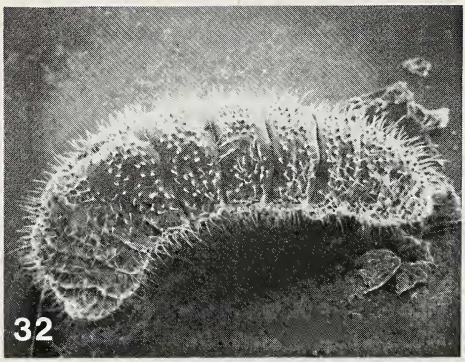


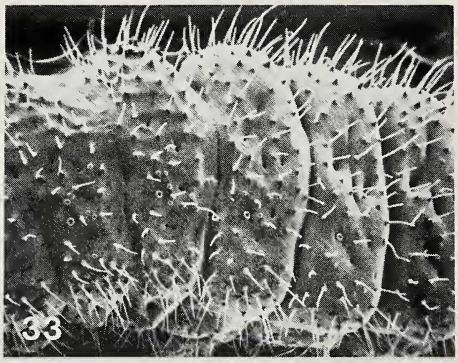


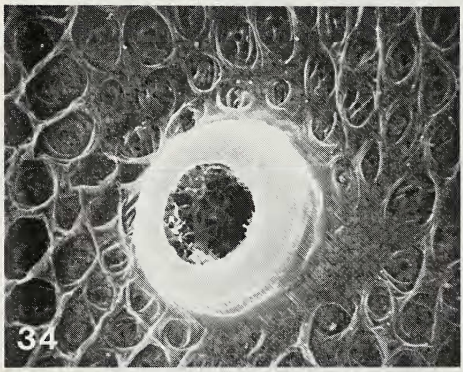


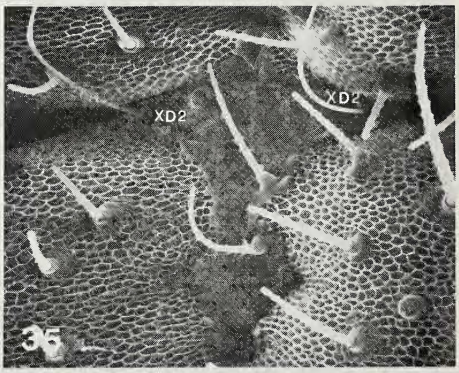


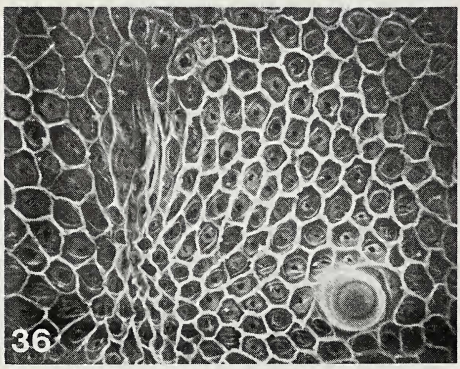
Figs. 26-31. SEM of second instar. 26. Whole larva, lateral view. Note holes eaten on undersurface of cranberry leaf. 40x. 27. Anterior end of larva. Prothorax with depressed shield. 80x. 28. Lenticle. 2500x. 29. Prothoracic shield. Anterior portion of shield at top. 450x. 30. Integument showing deep conical pits. 320x. 31. Integument sculpturing. Note depressed oval surface units. 1250x.

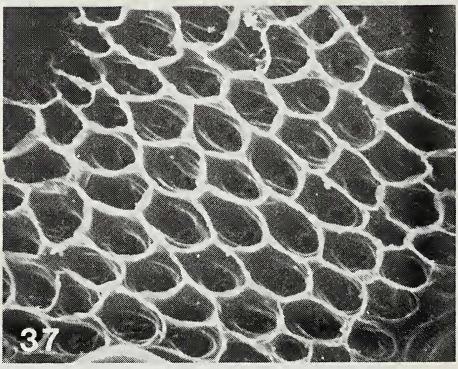




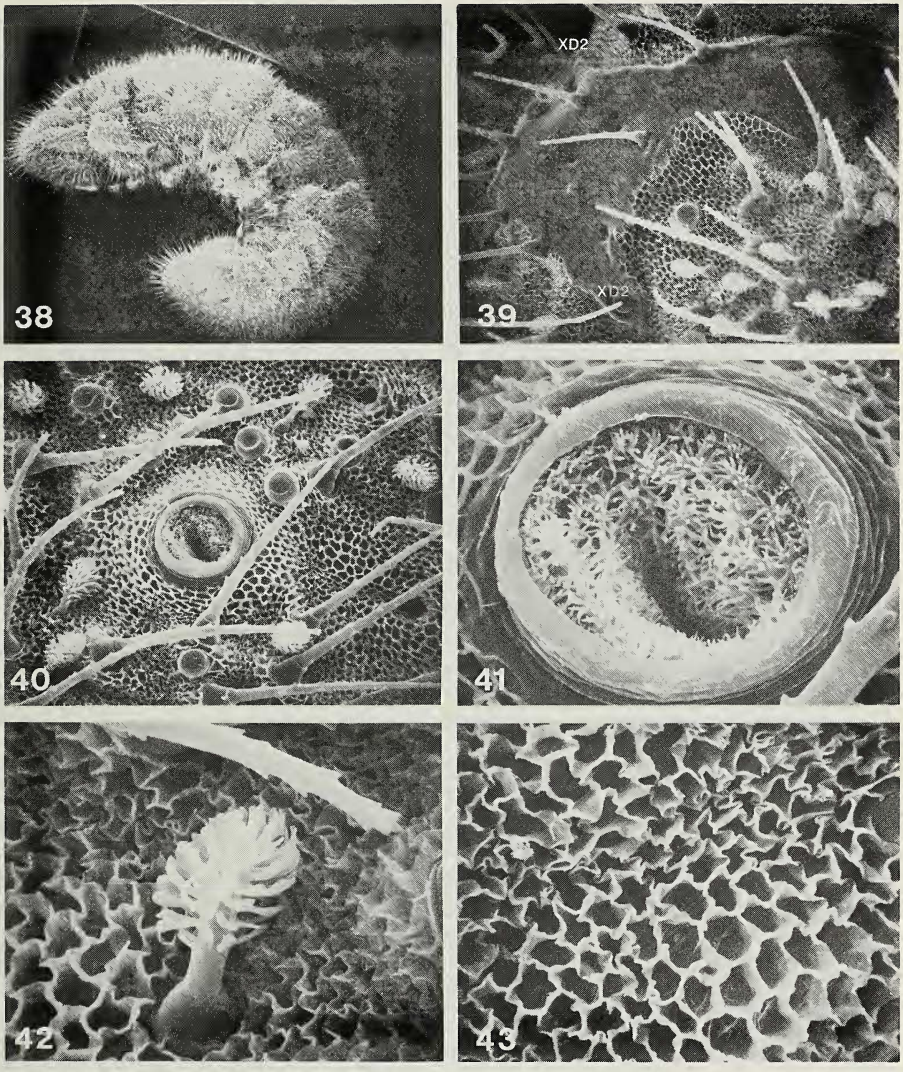




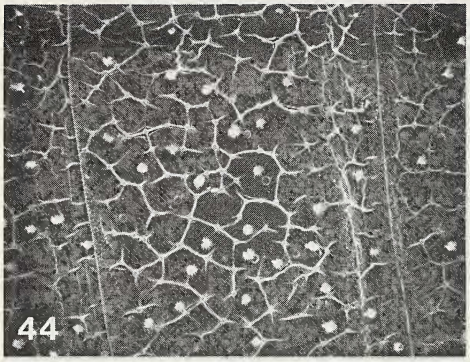


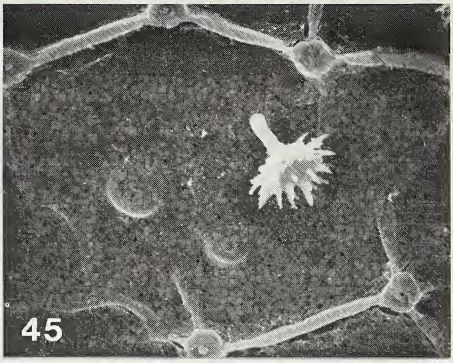


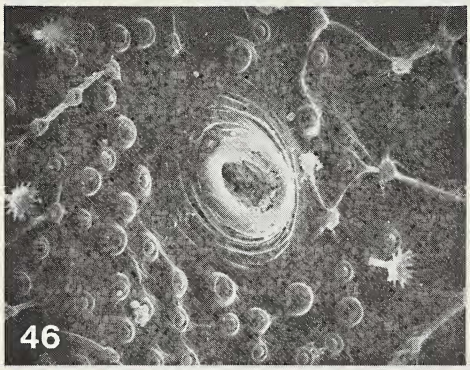
Figs. 32-37. SEM of third instar. 32. Whole larva, lateral view. Anterior segments on left. 20x. 33. Abdominal segments, lateral view. Note heavy secondary setation and integument pits. 46x. 34. Spiracle with internal sculpturing. 1250x. 35. Prothoracic shield. Anterior portion of shield at top. 240x. 36. Integument. Note pit in intersegmental groove. 640x. 37. Integument sculpturing. Note thin-walled partitions surrounding each surface unit. 1250x.

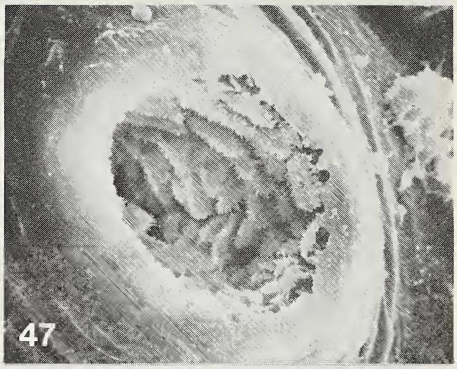


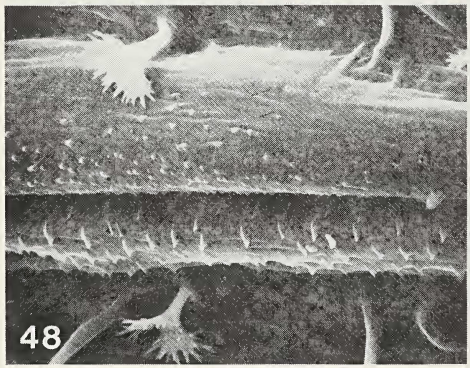
Figs. 38-43. SEM of fourth instar. 38. Whole larva, lateral view. Anterior segments at bottom right. Note extremely heavy secondary setation. 15x. 39. Prothoracic shield. Anterior portion of shield at left. 240x. 40. Integument showing spiracle surrounded by lenticles, major secondary setae, and specialized secondary setae. 320x. 41. Spiracle close-up showing internal sculpturing. 1250x. 42. Specialized secondary seta, "mushroom"-like. 1250x. 43. Integument sculpturing. Note tall thin-walled partitions surrounding each surface unit. 1250x.

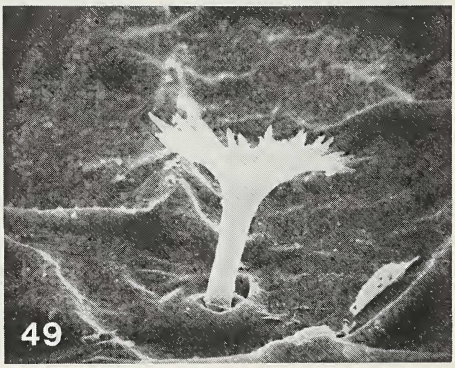












Figs. 44-49. SEM of pupa. 44. Pupal integument showing fine elevated ribs. 80x. 45. Integument close-up showing ribs, sensory verrucae, and seta. 640x. 46. Spiracle densely surrounded by sensory verrucae. 320x. 47. Spiracle close-up showing internal sculpturing. 1250x. 48. Stridulatory organ on intersegment A-5/A-6. Stridulatory plate at top (A-5) and file at bottom (A-6). 640x. 49. Pupal "trumpet-hair" seta. 1250x.